# THE
# AMERICAN NATURALIST

## ADAPTATION AND THE PROBLEM OF "ORGANIC PURPOSEFULNESS"[1]

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### I. THE REALITY OF THE PROBLEM

DESPITE the "revolutions of thought," which succeed one another with rather bewildering rapidity these days, we may occasionally listen with profit to the voice of a past generation. And I can not believe that we are yet in a position to wholly reject Herbert Spencer's well-known characterization of life as a "continuous adjustment of internal relations to external relations." Now it is this process of adjustment to which we give the name adaptation, and the special structures or functions by which the adjustments are carried out are called adaptations.

By earlier biologists and philosophers these facts of adaptation and adaptedness were regarded as among the most fundamental phenomena of life. It was facts such as these that furnished ammunition for Paley and a whole succession of natural theologians. It was these which Lamarck sought to explain by his theory of evolution through functional activity, and which Darwin attributed to the action of natural selection. And it is in this same realm of facts that the vitalists find their rea-

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[1] In its main outlines, this paper was written about five years ago. It was submitted for publication February, 1918, and since then has undergone relatively little revision. For this reason, adequate reference has not been made to certain recent papers.

sons for attempting to remove biology from its place among the natural sciences.

Now it is a curious circumstance that recent developments of the evolution theory have carried us continually farther from an explanation of adaptation. Natural selection, in the Darwinian sense, has been relegated to a secondary position, while the Lamarckian principle is denied *in toto* by many. On the other hand, all that the mutationist can tell us in regard to the matter is that such useful characters as spring full-fledged into existence are not likely to be eliminated. Thereupon, the vitalist takes fresh hope and asserts the inadequacy of what he calls "mechanistic" biology to account for progressive evolution.

Of course, one way to solve a problem is to deny that the problem exists. And this is what is being done by various persons who are interested in minimizing the difference between the living and the non-living. Thus one physiological botanist, Livingston,[1a] tells us that anything organic or inorganic is adapted to do just those things which in reality it is found to do. And he seems to think it quite as reasonable to speak of the adaptation of fragments of pumice to float on water, as of the adaptation of a flower to insure the visits of insects. The "concept of purposeful adaptation," which still plays such an extensive rôle in biology, is due to the fact that "ours is a developmentally young science," retaining "features of its early youth." Sooner or later this concept will be "totally abandoned, even as the same concept has already been abandoned by the other natural sciences."

Now it may well be that a more mature state of science will enable us to dispense with such naïve expressions as imply that an organ has a function to perform in the economy of an animal. And it may be that growing enlightenment will lead us to replace such a primitive notion as that of life by chemical affinities, electric charges and what not. But until that happy (or unhappy!) day

[1a] Aᴍᴇʀɪᴄᴀɴ Nᴀᴛᴜʀᴀʟɪsᴛ, January, 1913.

arrives, I think that most biologists will continue to regard the origin of adaptive characters in animals and plants as offering a real and important problem for solution.

Again, Parker,[2] while going to no such lengths as this in denying the significance of organic adaptation, expresses his belief that

the majority of animal reactions are, in all probability, neither conspicuously advantageous nor disadvantageous to the life of the individual. They are dependent chiefly on the material composition of the given organism, and, so long as they are relatively indifferent to the continuance of life, they pass without special consequence. . . . The world at large affords an environment in which each animal has a wide range for possible reactions, and of a number of responses that might be made to a given set of conditions, one may be quite as appropriate for the continuance of life as another. In other words, versatility seems to be a more truthful description of actual conditions in animal life than the rather rigid state implied in the idea of adaptive responses.

It may be freely granted that much ingenuity has been displayed in discovering adaptations which probably do not exist. And it is doubtless true that many organisms may live indifferently under a wide range of conditions, or may eat indifferently a wide range of foods. But is not this condition of versatility itself a fact of adaptation? The "continued adjustment of internal relations to external relations" implies that the external relations change. Man, it is true, may live indifferently on the equator or within the Arctic circle. But would any one maintain that the physiological states which adapted him to these unlike conditions did not differ widely in the two localities? I may make a meal equally well of meat or of vegetables. But the digestive fluids secreted for the occasion would differ in the two cases.

Again, because two wholly unlike plants grow side by side in the same soil, it does not follow that they are adjusted in quite diverse ways to the *same set of conditions*. The environment of an organism doubtless comprises the totality of things which surround it. But the *effective* environment comprises only those things with which

[2] AMERICAN NATURALIST, January, 1913.

the organism comes into functional relation. And as the organism evolves, these effective elements become different.

As I see the situation at present, the fact of organic adaptation remains the central one in evolution, and indeed the central one in biology. I shall give no further time, therefore, to justifying a rather laborious attempt to show how this fact may be accounted for without carrying us outside the limits of natural science. Before passing on to this discussion, I will merely remark that I place in the category of adaptation anything which increases the adjustment of the organism to the conditions of its existence, whether or not this may ever have a determining influence in the preservation of life. Many such adjustments have arisen in our own race which certainly can have played no part in the survival of the individual or the race. An example of this is the case dwelt upon by Spencer, of the correspondence between the nicety of tactile discrimination on various parts of our skin and the relative frequency of contact with foreign objects on these surfaces. And such cases could be multiplied indefinitely. Nevertheless, much recent biological speculation has been vitiated by the identification of adaptation with self-preservation.

## II. Adaptation and "Contingency"

If an intelligent animal is confronted with the necessity of taking action to avoid injury or secure food, two ways only would seem to be open to it:

1. It may consciously adapt its actions to this end, or
2. It may go through a series of more or less random movements until it happens to make one which is fitted to the needs of the situation.

On first thought, it might seem that these two modes of procedure were radically distinct, and indeed, in a sense they are. Considered historically, however, the second may be regarded as a step in the development of the first, or, to express the same thought otherwise, intelligent action is in every case the outcome of earlier experi-

mentation.   We can foresee the results of an action, only
in so far as they have been experienced before, either in
a situation identical with the present one, or at least in
situations having certain elements in common with it.
Furthermore, in the early life of the individual, the
movements of the so-called "voluntary" muscles were
in a high degree random and undirected.   The association
tion between a given muscular contraction and a given
result in consciousness must, in the first instance, have
been purely arbitrary, and could not have been antici-
pated prior to experience.

Thus to restate somewhat paradoxically our original
proposition, an intelligent animal attains a sought-for
end, either by blundering into it or by directing its course
on the basis of past blunders.   In either case, the asso-
ciation between the means employed and the end attained
is, in the last resort, accidental.   At the outset, the idea of
the end did not in any direct way call forth the means to
its realization, however purposive the action may appear
when fully perfected.

Let us extend our argument to those fields of organic
activity from which intelligence seems to be largely or
wholly excluded.   In instinctive actions, even more than
in intelligent ones, a series of movements proceeds unfal-
teringly to a given end, as if directed by the latter.   In
earlier days the adaptive instincts of certain lower ani-
mals furnished some of the most telling arguments for
the special interposition of an all-wise Providence.   To-
day, as biologists, we commonly explain these movements
on the basis of an inherited "mechanism."   We may be-
lieve, with Loeb and others, that we have to do with a
chain of reflexes, each serving as a stimulus to call forth
its successor at the appropriate moment.

How this mechanism arose is a disputed point, but
there are two principal hypotheses as to its origin: (1)
Instinctive actions are ones which originated, intelli-
gently or otherwise, in the course of individual expe-
rience, and finally became fixed through heredity; and

(2) they are the result of natural selection, acting on congenital tendencies toward such movements as proved to be adaptive.

Without discussing the merits of these rival theories, which are by no means mutually exclusive, I merely wish to point out that both of them assume a complete *contingency* as regards the relation of means to end. On the assumption that instinct is inherited habit, the actions, before becoming habitual, must have been performed either intelligently or as a result of blind groping. In either case, their adaptedness to the end in view was, at the outset, accidental, as we have already seen. On the assumption that instincts have arisen through natural selection, chance tendencies toward movements of an adaptive sort were perpetuated. Here, the complete contingency is obvious, unless we assume some directing influence determining the nature of the variations. I shall return to this last point later.

Still lower than instincts, in the scale of organic behavior, we have the various responses to stimuli which are known as "tropisms" or "taxes." Under this head are included the locomotion of the organism to or from a source of stimulation, or, in the case of a fixed organism, the assumption of a definite position, or the arrangement of its parts, with relation to the direction of the stimulus.

Here, again, we have two rival hypotheses, which are not, it seems to me, wholly antagonistic. According to one view, the organisms are "fatally" turned to or from the source of light, heat, or the like by the unequal stimulation of the opposite sides of the body. When the appropriate orientation has been brought about, the two sides of the organism are equally affected, and further locomotion will be in line with the source of stimulation.

The other view lays stress on those cases in which organisms are not drawn directly towards or away from a stimulus, but undergo random movements, having no primary relation to it. In what are regarded as the most primitive cases the stimulus which results in a change

of behavior is usually a noxious one, leading to a backing out or turning aside. When forward movement is resumed, it is a matter of chance whether the organism remains in favorable surroundings or finds its way back to the unfavorable ones. If the latter, the "avoiding reaction" recurs, and the performance is repeated until it leads to a more fortunate issue. The invariable "pull" or "push" of the tropism theory is not regarded as the primary phenomenon, though an observer who viewed only the end results of the process might easily believe that they had been brought about by such a directing influence.

Here, again, it is not my purpose to discuss the merits of these rival hypotheses. It is possible, indeed, that they should be regarded as complementary, rather than antagonistic. Jennings admits that responses which originally were performed according to the method of "trial and error" may, through the abbreviating influence of habit, come to be determined more directly by the stimulus. But, however we may view the method of origin of these responses to stimuli, it seems plain that any adaptiveness that we meet with is contingent in the sense in which I have already used the term. According to the investigations of Jennings, the organism reaches an optimum environment by chance, and remains there because it is stimulated to change its course whenever it begins to pass out of this environment. That unfavorable stimuli should provoke these changes of behavior need not be attributed to any "primary purposefulness" in living matter, since we can be perfectly sure that any organisms behaving differently would be speedily eliminated.

Again, I take it that the chief advocate of the theory of direct orientation would be the last to assume a principle of primary adaptedness, and would admit that any utility connected with these "tropisms" must have been, in the first instance, a pure coincidence. In the case of an organism, "irresistibly" drawn toward a favorable

stimulus, as a growing plant toward the light, we might seem to have an instance of such a directly purposive action, *i. e.*, the determination of the means by the end. But several things must here be taken into consideration. (1) It not infrequently happens that organisms are drawn in an equally irresistible manner toward a fatal stimulus, *e. g.*, the moth to the flame; (2) we can not feel sure, in every case, that the attainment of the goal is not the outcome of random movements, unperceived by the observer; (3) even where the response is indubitably adaptive, and as direct and unfailing as a simple reflex, it may be the outcome of a mechanism developed through natural selection, *i. e.*, the survival of random variations which were as frequently unadaptive as they were adaptive. The fact that some organisms still make suicidal responses to less familiar stimuli favors this last view.

Next, we may consider the phenomena of metabolism, growth and development. We group these things together, because they can hardly be considered separately. Growth is the outcome of metabolism, and development of metabolism and growth.

The phenomena revealed through studies of normal physiology and embryology are obviously highly "purposive," in the sense that they have relation to the attainment of an end, that end being the preservation of the individual and the race. Nevertheless, they are believed by most biologists to be the outcome of a "mechanism" the functioning of which presents no greater difficulties, apart from complexity, than the working of a clock or a steam-engine.

When we come to consider the origin of this mechanism, we may mention three chief hypotheses, which have been or still are held. (1) It may have been specially created by a super-mundane power in each individual species of organism; (2) it may have gradually developed out of simple beginnings by the "selection" or survival of random variations which were as likely to be unadaptive as adaptive; or (3) it may have gradually

developed out of simple beginnings through (*a*) direct responses to environmental stimuli, or (*b*) the effects of functioning upon the functioning parts themselves.

The first of these alternatives has been well-nigh discarded by scientist and layman alike, and need not be further considered here. I will point out in passing, however, that certain elements of the "special creation" hypothesis have recently been put forward in the name of science. Of this more anon.

The second alternative, that of natural selection, is admitted by most biologists to be one of the factors concerned in the production of adaptive mechanisms, though it is doubtful whether any two thinkers would agree as to the importance to be assigned to it. The essence of this hypothesis is the contingency of the individual variations in relation to the need to be satisfied. If the variations are *directed,* in the sense of tending preponderatingly toward the satisfaction of this need, then our explanation is shifted to a totally new basis. It is this directive tendency, not natural selection, which is the effective agency in evolution. The consequences which would follow such an assumption will be discussed later.

The third of our alternative hypotheses has figured historically as the chief rival of natural selection, though by many (*e. g.*, by Darwin himself), both principles were accepted. One of the merits of the Lamarckian principle, in the eyes of some of its adherents,[3] is its apparent rejection of contingency or chance, a fatal weakness, so they believe, in the natural selection theory. But a little thought will show us that the Lamarckian principle, no less than the Darwinian, is based upon chance, as regards the relation between the need and the means to its fulfilment.[3a]

[3] August Pauly, "Darwinismus und Lamarckismus," 1905; R. H. Francé, "Der heutige Stand der Darwin'schen Fragen," 1907.

[3a] It is true that both of the writers cited in the preceding footnote clearly recognize this *accidental* character of adaptive responses in their inception, though failing to realize the significance of this fact for biological philosophy. (See my review of Pauly, in *Journal of Philosophy, Psychology and Scientific Methods*, August 27, 1908.)

Let us consider (*a*) the case of modification through direct environmental stimuli.  There is much vague talk about the "environmental mould," in which the "plastic" organism is supposed to be "cast"; but those who have given much study to the subject recognize that modifications produced by the environment are in the nature of reactions to stimuli.  In many cases, these reactions are plainly adaptive, in the sense of furthering the life or comfort of the individual or the race, as when a callosity is developed in consequence of continued friction, or an antitoxin is generated to combat a bacterial poison. The fact, however, that there are varying degrees in the adaptiveness of these responses, and indeed that many of them appear to be wholly unadaptive, suggests the probability that the truly adaptive ones, when at all constant, have resulted from the selection of "accidental" variations.  This can, of course, be true only of responses to environmental stimuli which have presented themselves frequently in the history of the race.  Cases in which the organism has responded adaptively to stimuli quite new to racial experience are not, however, entirely unknown.  These will be discussed in a later section.  It may be said in passing, however, that the only conceivable scientific explanation of such cases involves the principle of "trial and error," which, of course, is based upon complete contingency as regards the relation of means and end.

Let us pass to (*b*) the effects of functioning upon the functioning parts themselves.  It is held by the Lamarckians that organs or parts grow or diminish through use and disuse, and that the perfected mechanisms which now arouse our admiration and wonder are the outcome of past functional activity.  Many upholders of this view introduce the idea of a conscious struggle toward a desired end.  The perfecting of the parts they regard as a voluntary process.  Thus is "blind chance" cast out as a factor in evolution.  But such reasoning rests on insufficient analysis.  Granting the part played by voluntary action (*e. g.*, exercise or practice) in the post-

natal development of many higher organisms, we need only refer the reader to what we have already said about the "contingent" character of even intelligent action. But it seems likely that the claims of the psycho-vitalists (*e. g.,* Pauly and Francé) are largely fantastic, and that voluntary struggle toward an end has not played the important rôle in organogenesis which they imagine that it has. The greater part of the functioning of the organism probably consists in blind responses to external or internal stimuli—blind in the sense of having no conscious end in view. Thus regarded, they are in no way different from the responses already considered under (*a*), save that we there dealt with the effects of external stimuli alone.

Accordingly, we may repeat here that so far as these functional responses—and the organs they perfect—are adaptive, their adaptiveness must have arisen, in the first instance, by the selection of contingent variations. Under this head are to be included (1) the preservation of those individuals which chanced to make appropriate responses (natural selection); and (2) the making habitual on successive generations of individuals of responses which chanced to fulfil a given need when first experienced (Lamarckism). The only other alternative would seem to be some sort of inscrutable foreknowledge on the part of the organism of every need to be experienced, and of the way in which this need could be satisfied. Such a conception would obviously carry us beyond the field of scientific explanation, but I shall none the less consider it in its proper place.

It is not my purpose here to discuss the arguments for or against either the Darwinian or the Lamarckian principle. It is my object merely to point out that *both theories rest on the selection, in one way or another, of variations which were originally contingent or accidental, in the sense of not being directly determined by the need to be fulfilled.* And, indeed, this is true of all of the other rival or subsidiary hypotheses of evolution,

so far as they may be regarded as scientific theories at all.

The theory of mutation, in its original form, postulated large and abrupt variations as the material for selection, a modification which does not affect the principle essentially. In its later form, it merely insists that these variations must be of the discontinuous or Mendelian type, assuming that all other variations are non-inheritable. Those who maintain the importance of isolation in evolution can not, of course, regard this as a *vera causa* of adaptive change. The actual changes must be either "spontaneous" variations or mutations or else modifications due to environment. Thus, we must resort finally to either the Lamarckian or the Darwinian principle to account for such of them as prove to be useful. "Orthogenesis," so far as it is not a vague appeal to a "perfecting principle," "élan vital" or the like, is a mere assertion that variations may accumulate in a given direction independently of selection. Wherever the variations are sufficiently adaptive, however, we are not justified in excluding selection. When non-adaptive, such a process presents no greater difficulty in principle than the continuous growth of a crystal or the continuous deepening of a canyon by erosion.

Most of us are prepared to admit that much in the organic world is non-adaptive. We may even grant that a large proportion of the diagnostic characters of species and genera belong to this category. Such characters, while they may baffle the investigator, are in general not such as would have suggested the operation of a supernatural factor in evolution. In this paper we are concerned with the problem of organic adaptation, and shall leave aside the origin of characters which are useless to the organism.

*In the foregoing analysis, I have regarded adaptive response, whether of structure or function, as being invariably a secondary phenomenon. The connection between the need of the organism and the means adequate to satisfy this is believed to have always been, at the out-*

*set*, an "accidental" one. In those cases where the correct response appears to ensue unhesitatingly, we have had to suppose either (1) that the observer has overlooked "trial and error" stages preceding the response in question, or (2) that the response is the outcome of an inherited mechanism, based upon racial experience, and therefore ultimately upon some form of selection.

### III. Vitalism[4]

Let us now consider the claims of a school of thinkers who argue for the existence of a primary purposefulness in living things, and who deny that any conceivable mechanism can account for certain of the phenomena observed. As the most conspicuous representative of this school we naturally turn to Hans Driesch, who has made a more determined attempt than any other vitalist to reduce his beliefs to a unified system of philosophy.

Driesch's three "proofs" of vitalism may be summarized as follows:

1. In the earlier development of some organisms, rather low in the scale of life, any part of the embryo, provided that it be of a sufficient size, will, if artificially detached, produce the entire organism. This he regards as conclusive disproof of the supposition that the spatially arranged diversities of the adult organism depend for their origin upon diversities of a *spatial* sort in the embryo. Such a spatial prearrangement of the parts as is postulated by the Weismannian "germ plasm" theory, and other preformationist hypotheses, he assumes to be essential to any mechanical theory whatever.

But, Driesch claims, the spatial diversities of the adult organism must depend upon preexisting diversities of *some* sort, therefore he invokes a non-spatial agent, "entelechy," to account for them. Now "entelechy" must be a manifoldness, since it is conjured up to explain other manifoldness, but this manifoldness is *intensive*,

[4] In this section, I have made free use of a review of Driesch's "Science and Philosophy of the Organisms," which I wrote some years ago (*Journal of Philosophy, Psychology and Scientific Methods*, June 9, 1910). I have not thought it necessary, however, to indicate the extent of these quotations.

not extensive.    As an illustration of an "intensive mani-
foldness" he instances one of our own states of con-
sciousness, in which many elements are presented simul-
taneously, though not spatially separated from one an-
other.    But entelechy is not to be identified with mind.
It is an unknown something which stands in the same
relation to our mental life as it does to other organic
phenomena.

2. Driesch's next "proof" of vitalism is somewhat
similar to the first, though it rests upon the facts of nor-
mal life history, instead of upon artificial disturbances
of this.    The primitive germ cells, each of which, accord-
ing to the hypothesis he combats, should contain the
"machine" or spatial prearrangement of parts neces-
sary for the development of an entire organism, undergo
in the gonads an extensive series of divisions, leading to
the formation of the mature ova and spermatozoa.
"Can you imagine," he asks, "a very complicated ma-
chine, differing in the three dimensions of space, to be
divided hundreds of times and in spite of that to remain
always the same whole?"[5]

3. The last "proof" of vitalism is based upon an anal-
ysis of animal behavior.    Driesch makes much of the
fact that an action of a higher animal, particularly of an
intelligent one, is something more than the sum of many
simpler elements, each depending upon an element in
the complex of stimuli to which the organism responds in
a given case.    The response of the organism is a unified
whole, corresponding to a total situation in the outer
world.    A slight change in this complex of physical stim-
uli, provided that it has *significance* for the organism,
may result in a totally different kind of response.    On
the other hand, an entirely different set of physical ele-
ments—having, however, the same *meaning* for the or-
ganism—may call forth precisely the same response.    In
other words, there is no functionality (in the mathemat-
ical sense) between the response and the stimulus.

This line of argument, different as it may seem, rests

5 "Science and Philosophy of the Organism," Vol. I, p. 225.

upon the same fundamental assumption as the two preceding ones, namely, that a truly mechanical theory must find in the cause as many separate elements as we observe in the effect. The structural diversities of the adult organism must rest upon corresponding structural diversities, present from the beginning in the germ. The functional diversities, constituting a complex act of behavior must rest upon corresponding functional diversities in the stimuli which make up the total effective situation. If no such correspondence can be shown, we must invoke some principle of a totally different nature from those which we employ as explanations in the inorganic world.

Now, such a conclusion as this seems to rest upon an insufficient consideration of what really happens in the inorganic world. In a sense, the solar system was present potentially in the original homogeneous nebula, while the various continents and oceans, mountains, lakes and rivers of the world we live in were all present potentially in the molten globe which in some way detached itself from the parent mass. But there was certainly no ''preformation'' of these final products of cosmic evolution. The diversity which was introduced was totally new. In the language of biology the world's development was strictly ''epigenetic.'' And yet the process was none the less mechanical, as every vitalist will allow. Why then does Driesch insist that a mechanism adequate to account for an animal's ontogeny must present a part-for-part correspondence with the adult organism? For it is only a mechanism, *as thus conceived,* that is disposed of by his ''proofs'' of vitalism. His experiments compel him to dismiss the notion of a *spatial* prearrangement of parts. Therefore, he jumps to the conclusion that there must be a *non-spatial* prearrangement of parts—an ''intensive manifoldness.'' But why should there be any prearrangement of parts at all? Is it not a fallacious philosophy which insists on such an exact numerical cor-

respondence between the elements of the cause and the elements of the effect?[6]

Despite these logical difficulties, Driesch's third "proof" of vitalism contains such an unmistakable element of plausibility that some further consideration may profitably be given to it here. His contention is summed up in the phrase "individuality of correspondence" between stimulus and reaction. "It is not the single constituents of the stimulus," he says, "on which the single constituents of the effect depend, but one whole depends on the other whole, both 'wholes' being conceivable in a logical sense exclusively" (II, 81). Why is it that we react to *objects* rather than to sensuous images? "The dog, 'this dog,' 'my dog,'" to quote Driesch, "is 'the same' stimulus, seen from any side or at any angle whatever: it always is recognized as 'the same,' though the actual retinal image differs in every case" (II, 73). Experience and association, he thinks, afford an insufficient basis of explanation here. There must be something capable of resolving past experience into its elements and making wholly new combinations of them.

Driesch challenges his opponents even to conceive of a machine that could accomplish results such as these. This introduction of the word "machine" would seem to prejudice the case in his favor at once. But is he not really challenging us to imagine how phenomena that require sense organs and a nervous system for their performance could be performed by some other type of mechanism which is simpler and more fully understood by us. Confessedly we can not do so. Looking at the subject in an unbiased way, it would seem that the nervous system had the appearance of a finely wrought mechanism to a higher degree than any other portion of the body. It is truly one of almost infinite complexity, and one that is largely inaccessible to experimental observation. But certain significant facts have been demon-

[6] Spaulding (*Philosophical Review*, July, 1909) and Jennings (*Johns Hopkins University Circular*, No. 10, 1914) have already called attention to the fallacy of this aspect of Driesch's argument.

strated none the less. Sherrington has described in
some degree the mechanism of inhibition, and has ascer-
tained some of the factors which determine which of two
simultaneous stimuli shall prove effective in a given re-
flex.   Do not such data at least help us to conceive the
possibility of a nervous system whose activities may be
understood without the aid of an entelechy to make its
decisions for it?

The emancipation of the organism from the controlling
influence of immediate stimuli is admitted to be one of
the salient features in animal evolution.   Now, in order
that present activities may be directed with reference to
future results, the stimuli must become more and more
symbolic, *i. e.,* they must acquire a ''meaning.''   That
one thing may ''stand for'' something else, and call up
the responses proper to that something else may readily
be understood in terms of association.   At least there
would seem to be no desperate need for invoking ''en-
telechy'' at this point.   If this be granted, why should
we expect any correspondence between the sensuous ele-
ments of the stimulus and the elements of the response?
The effects of a given ''individualized stimulus'' are de-
pendent rather upon the aggregate of associative proc-
esses which this stimulus calls up.   And this aggregate
is altogether an empirical one, not a logical one as
Driesch supposes.   The connections that bind it together
may be quite arbitrary and accidental.   It is partly the
product of individual experience, partly of racial expe-
rience—this last on any theory of inheritance.   That
several widely different stimuli, having the same mean-
ing (*i. e.,* having certain important associations in com-
mon), can bring about essentially the same response
would seem, on the face of it, no more difficult to under-
stand ''mechanically'' than that several very differently
shaped keys can open the same lock.

The weakness of Driesch's ''third proof of vitalism''
would seem, therefore, to be twofold.   (1) He appears
to believe that an explanation, in order to be mechanical,

must find a definite correspondence between separate factors of the cause and separate factors of the effect,[7] and (2) he appears to believe that in any mechanical explanation of action the character of the response must be determined by the immediate sensuous stimuli themselves, without regard to the representative (associational) character of these stimuli.

Driesch, like other vitalists, lays great stress upon "adaptive" or "regulative" phenomena, though he makes no claim that these necessarily demonstrate the truth of vitalism. Indeed, it will be noted that the three foregoing "proofs" rest on quite other grounds. We may safely say, however, that for most biologists the great stumbling-block to a consistent mechanical explanation has been this central fact of organic "purposefulness." In pre-Darwinian days the whole subject was a mystery, which science cheerfully handed over to theology for solution. Later, we grew accustomed to the idea that much which seemed purposeful in nature was the outcome of "chance." But for many there was always a considerable residuum which defied solution. For there certainly seem to be cases of adaptive response to wholly new situations, that can not be accounted for on the basis of an evolved mechanism. And furthermore, it is now obvious that no single theory of evolution yet proposed, nor, indeed, all of them combined, can adequately account for much that has come to pass.

In the face of these perplexities, it is but natural that many have taken refuge once more in various intangible forces and principles, almost wholly devoid of positive attributes, and agreeing only in their alleged competence

[7] It must be admitted that explanations of this type have been put forward by avowed mechanists. Thus Loeb ("Mechanistic Conception of Life," p. 80), in discussing the present writer's experiments upon the color changes of flatfishes, concludes that there is an actual reproduction on the skin, through the brain, of the retinal images of the background. I think that a careful reading of my own discussion of these experiments sufficiently disposes of this contention (*Journal of Experimental Zoology*, May, 1911). The yet more extensive experiments of Mast (*Bulletin of the Bureau of Fisheries*, Vol. XXXIV, are likewise conclusive against this view.

to "explain" otherwise inexplicable facts. Of these Driesch's "entelechy" and Bergson's "élan vital" are but types.

Much less discordant with our scientific habits of thought are the utterances of some of the so-called "psycho-vitalists," to whom allusion has already been made. These writers do not have recourse to metaphysical principles, wholly beyond the realm of experience. They invoke the familiar facts of conscious purpose, intelligence and will. Organic happenings *seem* purposive, they think, because they *are* purposive, in the same sense that our own voluntary actions are purposive. Such a view carries the realm of mental life far beyond the bounds which we are wont to assign to it. Its logical outcome is a thoroughgoing panpsychism, an outcome which some of its advocates are quite ready to accept.

Now, it seems to the writer that a panpsychic view of nature can be stated in such terms as not only to be plausible, but to meet certain of our most fundamental intellectual needs. But such a view is at best a philosophical creed, not a scientific explanation, and should never be offered as a substitute for the latter.

The introduction of will, purpose, etc., in the rôle of scientific explanations may have one of two implications. Either (1) it may be assumed that a given physical configuration, plus these psychical concomitants, is able to accomplish what would be impossible for the *same* physical configuration minus these psychical concomitants (interactionism); or (2) it may be assumed that only that type of physical configuration which is invariably bound up with certain psychical factors is competent to call forth the result in question (parallelism). According to the second point of view, the question whether the same result would have ensued without the agency of purpose or will is an absurdity. If purpose and will had been lacking, the physical antecedents would of necessity have also been different.

It is needless to say that both of the foregoing positions have been upheld by philosophers. It is my wish

to point out, however, that on neither assumption does the introduction of conscious purpose supply a missing link in our explanation of the "teleological" in nature. Whether or not we admit the efficacy of mental states, independently of their physical concomitants, we have already seen that conscious purpose must proceed on the basis of experimentation. It must have learned through trial that a given means will lead to the attainment of a given end. The existence of any primary foreknowledge of the relation of means to end is contradicted in our own every-day experience.

It may be useful to introduce a description by a psychologist[8] of what actually occurs when we are trying to solve a problem:

Our only command over it is by the effort we make to keep the painful unfilled gap in consciousness. . . . Two circumstances are important to notice: the first is, that volition has no power of calling up images, but only of rejecting and selecting from those offered by spontaneous redintegration [= association]. But the rapidity with which this selection is made, owing to the familiarity of the ways in which spontaneous redintegration runs, gives the process of reasoning the appearance of evoking images that are foreseen to be conformable to the purpose. There is no seeing them before they are offered; there is no summoning them before they are seen. The other circumstance is, that every kind of reasoning is nothing, in its simplest form, but attention.

It is, therefore, a false theory of our own purposeful actions that is projected backward into organic nature by the psycho-vitalists. The existence of instinctive acts, which fit means to ends, prior to experience, in no way invalidates what I have said. For these may be assumed to be based, in some way, on past racial experience. And, in any case, so far as an action is instinctive, it can not be *consciously purposive*. Assuming that instinctive actions are performed consciously, at all, which some would perhaps deny, it is not likely that anything beyond the next succeeding step in the series is at any moment present to consciousness. The biological meaning of the entire performance (say the building of

8 Hodgson, quoted by James ("Principles of Psychology," Vol. I, p. 589).

a nest) can not be understood by the organism.   Each step is desired and willed on its own account alone.   The end *takes care of itself*, by virtue of a preestablished mechanism.

Thus purpose, in the psychological sense of the word, can not be predicated of a complex instinctive act, even though the individual steps be consciously performed. Least of all can it be predicated of a process of organic regulation or reparation, the object of which can never be consciously in view.   It was doubtless in part considerations like these which led Driesch to deny the mental nature of "entelechy" altogether and to remove it to a transcendental sphere in which it was no longer subject to the exacting demands of experienced reality.   Indeed, he tells us that "there *must* be a something in them [morphogenetic, adaptive and instinctive entelechies] that has an analogy not to knowing and willing in general . . . *but to the willing of specific unexperienced realities,* and to knowing the specific means of attaining them" (II, p. 142).   We think more favorably of Driesch's good sense when he admits that the position of his doctrine is at this point "rather desperate."   Nor is Bergson's case a bit better when he naïvely attempts to clear up certain of the most baffling phenomena of instinct by invoking the aid of "intuition" or "sympathy."[9]   The psycho-vitalists introduce an agent which is to some degree intelligible, even though it is inadequate.   The agents which Driesch and Bergson conjure up are neither adequate nor intelligible.

In the writings of these and some other vitalists the "vital principle," by whatever name called, is distinctly credited with powers which we should ordinarily term clairvoyant.   Indeed, we are forced to conclude that it must be able to "tap" sources of information which are closed even to the highest finite intelligence.   This, of course, is mysticism pure and simple, though such a reproach admittedly does not constitute its refutation for all minds.

[9] "Creative Evolution" (trans.), pp. 173–175.

It may be interesting perhaps to consider where such assumptions would lead us. Suppose that we adopt the absolutist idea of an Infinite Knower, having cognizance of the future as well as the past, or rather including both future and past in one eternal present. By getting into connection with this, our entelechy could doubtless solve any problem which confronted it. But how, on such an assumption, could we account for the multitudinous *mis*-adaptations which confront us? How should we explain an instinct which led to the harboring of baneful parasites in an ant community or a regenerative process which resulted in the formation of the wrong organ? Perhaps these perplexing cases would be merged into the general mystery of the origin of evil, and there, indeed, may be where they belong.

But we are not compelled to accept an absolutist interpretation of things. As scientists, we may find it more easy to believe in the evolution of God, in a *"Dieu qui se fait."*[10] Well and good, but then the essence of this view is the *newness* of everything that happens. No mind, however infinite, could foresee the future, for the simple reason that the future is not determined until it comes to pass. Even our deity must learn by experience, and "entelechy" would have to do the same. In that case neither would be of much service in attempting to explain organic purposefulness. Had we previously learned to expect any great amount of consistency among the various views of M. Bergson, it would have been a source of surprise to us to find him coupling together this idea of "creative evolution" with a transcendental "élan vital," which provides the organism with useful structures without the guidance of experience.

Such a departure as I have made from the field of legitimate scientific discussion may shock those of my readers who shy at anything suggestive of metaphysics or theology. But we have been told with increasing frequency of late that our accepted scientific methods

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[10] I believe that this expression is Bergson's.

have broken down in the face of vital phenomena, and that the only path of escape was one which logically led to mysticism. For this reason it seemed worth while to inquire whether even this abandonment of our scientific principles would lighten our difficulties.

Now, while we believe the solutions offered by the vitalists to be but pseudo-solutions, we must admit that the issues they have raised are real ones. It is to the great credit of this school, and of Driesch in particular, that they have awakened some of us biologists from our "dogmatic slumber" and forced these problems upon our attention. The problems are real ones in the pragmatic sense of determining our attitude, both theoretical and practical, toward biological investigation in general. Most important of all, vitalism has unearthed a number of highly interesting experimental data, which it challenges its opponents to explain. To this extent it may lay claim to the rank of a "working hypothesis."

Let us consider some of the points at issue between vitalism and what I shall call "scientific biology." In what follows, I have stated what I believe to be the typical attitude of each side, though it is likely that no two persons would agree in every particular.

1. Scientific biology is strictly deterministic. It admits the possibility of only one result from a given set of antecedents. Vitalism is indeterministic, holding that from precisely the same antecedent situation more than one result is possible. Driesch saves the principle of "univocal determination" by saying that in cases where different results follow the same physical causes, there must have been a difference in "entelechy." But Johnstone,[11] a disciple of Driesch, throws over even this formal adherence to scientific method, and asserts boldly that there must be "uncaused differences" in the organic world. He illustrates this belief from the variability among the millions of eggs spawned by a single flounder. The usual explanation, based upon differences in exter-

11 "The Philosophy of Biology," 1914.

nal conditions or on imperfections in the mechanisms of cell-division he holds to be inadequate. Now, in his belief, it is these ''spontaneous'' variations (using the former word literally) that furnish the raw material for evolution.

Jennings[12] sees in this postulate of indeterminism the fundamental fallacy of vitalism. It certainly is the feature that would most seriously affect us as investigators. For whether variations are regarded as uncaused or as caused by an agent beyond the ken of scientific investigation matters little. Any attempt to account for them by experimental or observational means must be futile.

2. Scientific biology endeavors to explain organic phenomena on the basis of antecedent physical conditions, though admitting that our knowledge of cause and effect is in the last resort empirical, to the extent that much which happens could not have been predicted in advance. Vitalism explains organic phenomena—or a certain part of them—on the basis of ends to be realized, and gives to these ends a determining influence in providing the means to their realization. Since the *a tergo* ''push'' of physical causation would only by rare chance be directed in harmony with these ends, vitalism introduces a nonphysical agent to guide or control the former. Driesch goes to great lengths to explain how ''entelechy'' can play this rôle without coming into conflict with the law of the conservation of energy.

In a certain sense the existence of such ''ends'' must be admitted by all biologists. Attainment of the typical form, self-preservation, racial preservation, etc., are ''ends'' in the sense that organic processes in general are observed to trend in those directions. Furthermore, disturbances of this normal trend often seem to be corrected automatically. Phenomena strictly analogous in this respect can, of course, be instanced from the inorganic world. All we have to do is to designate the observed goal of such a process as the ''end'' and the

[12] *Science*, June 16, 1911; October 4, 1912.

causally determined steps become the means to its realization. The difference between such a physical process and a vital one, as conceived by Driesch, is that in the latter a given sequence of events *may or may not* come to pass, depending on the whim of "entelechy." The issue here, then, is practically the same as that first raised, namely, that of determinism versus indeterminism.

3. Scientific biology declares that vital phenomena are chemico-physical, in the sense that they are the inevitable outcome of the particular material aggregations which we term organisms.[13] It grants that in these manifold chemical syntheses entirely new properties have emerged, though insisting that the same may be said of any union of elements whatever. Vitalism denies that any possible configuration of material particles, without the aid of an immaterial principle, can account for the phenomena observed. It is for this reason that "vitalism" is commonly set in opposition to "mechanism." Driesch's three "proofs" of vitalism are concerned with this last aspect of the theory. We have seen that all three are based on the assumption that we must find a diversity in the cause, corresponding to each diversity in the effect. And it has been pointed out that this does not hold true even of admittedly physico-chemical systems.

Now, I do not claim that the bare word "mechanism," however hallowed by scientific usage, has any greater explanatory value than "entelechy." Indeed, I do not see why we should be called on to furnish a *mechanical* explanation, *sensu stricto,* of biological phenomena at all. Not all natural science is mechanics; some of it is chemistry. And I believe it is equally true that still another part is biology, a science quite distinct from either. But I think we can claim the possibility of a scientific explanation in the sense indicated by the foregoing antitheses, and it is with this in mind that I have grappled with the problem of organic "purposefulness."

(*To be concluded*)

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13 It is not, however, necessarily "materialistic" in a metaphysical sense.

# GIGANTISM IN NICOTIANA TABACUM AND ITS ALTERNATIVE INHERITANCE

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## Introduction

WITHIN recent years observers working with different varieties of *Nicotiana tabacum* grown commercially in the United States and elsewhere have recorded the sudden appearance of occasional giant plants of abnormally high leaf number. Except in height and number of leaves, which may be increased several times above the usual number, these giant plants in general appearance do not depart widely from the varietal type from which they took their origin. The great increase in number of leaves, together with a greatly elongated main stem, is accompanied by a period of vegetative vigor of such long duration that blossoming does not normally take place when the plants are growing in the field. In order to obtain seed from such plants, the usual practise has been to transplant the roots and stub, or even the plants entire, to the greenhouse in the fall, where vegetative vigor is resumed with the final production of normal blossoms and seed during the winter. Plants of this habit of growth have been recorded in the Sumatra, Maryland. Cuban and Connecticut Havana types of tobacco.

## Occurrence of Gigantism in Different Varieties

The first published record of gigantism in tobacco appears to have been made in 1905 by Hunger (1905), working with tobacco in Sumatra in connection with an investigation of the mosaic disease.

Garner (1912) mentioned a Maryland Mammoth type, the origin of which was associated with a cross between two common varieties of Maryland tobacco.

Hayes and Beinhart (1914) reported the occurrence of

giant plants in the Cuban shade tobacco and the Connecticut Havana type in Connecticut.

In addition to Hunger's observation previously mentioned, Honing (1914) brought out other interesting facts concerning the occurrence and behavior of giant plants in Sumatra (Deli) and Java.

Hayes (1915) further discussed the occurrence of giant plants in the Cuban and Connecticut Havana types of tobacco grown in New England.

Hunger, in the paper referred to, states that the largest giant plant observed by him developed 123 leaves and reached a height of nearly five meters. These plants were entirely sterile, or, if blooming took place, the number of blossoms was greatly reduced. Honing states that the behavior of these giant Sumatra plants with respect to the transmission of their peculiarities is variable. In one instance he observed that a line of these plants finally disappeared entirely. With respect to number of leaves, Honing's studies of the Deli tobacco indicates that several more or less distinct types exist. Even though line selections of these have been grown under bag for several generations, plants possessing high leaf number have occasionally appeared. Mammoth plants have also appeared in the Sumatra variety grown in the United States from seed obtained from Sumatra. In 1912 two plants of this type appeared in a plot of about 100 plants grown at Arlington, Va. These plants appeared in the second year's planting from seed obtained from Sumatra. One of these, when removed to the greenhouse, had reached a height of eleven feet and had produced about 100 leaves, with no indication of blooming. It was not possible to determine to what extent these plants transmitted their characteristics to their progeny since both died after being cut back and removed to the greenhouse.

In 1906 and 1907 giant or mammoth plants were obtained in Maryland tobacco, as mentioned above.[1] The

[1] A discussion of the commercial value of these types of Maryland tobacco will be found in Bulletin 188, of the Maryland Agricultural Experiment Station, entitled, "Types and Varieties of Maryland Tobacco," by W. W. Garner and D. E. Brown, 1914, pp. 135–152.

type known as the Broadleaf Mammoth was first observed in 1906 in a selection line of Maryland Broadleaf begun in 1904. Of 100 plants grown in 1906, five were typical mammoth plants producing many leaves and showing no tendency to bloom at the end of the season. Subsequent generations of these plants were grown successively in 1907, 1908 and 1909, and all reproduced the characteristic habits of growth of the original parent isolated in 1906. This mammoth type, as the name indicates, differed materially in shape of leaf from the better known Narrowleaf Mammoth.

The so-called Narrowleaf Mammoth appeared in 1907 in second generation plants of a cross made in 1905 between a Broadleaf type and a Narrowleaf type of Maryland tobacco. From a single mammoth plant found in 1907, 157 plants were grown in 1908, all of which were mammoth plants. Two of these plants which were allowed to grow until frost without topping had produced 109 and 111 leaves, respectively, with no indication of blooming. The Narrowleaf Mammoth has been propagated from seed and grown on a commercial scale in Maryland up to the present time, and under normal field conditions still retains its characteristics of high leaf number and the non-blooming habit.

A third mammoth type appeared in 1907 in second generation plants of a cross made in 1905 between Maryland Broadleaf and the White Burley variety of Kentucky. In a crop of 30,000 to 40,000 plants but one mammoth plant was found. Unfortunately, this plant was harvested inadvertently by laborers and lost.

From the previous discussion it is evident that gigantism has occurred rather widely in the varieties of *Nicotiana tabacum*. It would appear from Honing's work that Mammoth Sumatra plants are not constant in their inheritance and that intermediate forms exist. The accumulated experience of various observers working with all Mammoth types which have appeared in the United States, however, has shown a constant inheritance of

Mammoth characteristics from generation to generation. Intermediate forms have not been observed.

### Behavior of Gigantism in Crosses

Since Mammoth forms are now grown commercially in the United States and promise to become valuable new varieties, it has been considered desirable to determine the possibility of combining the Mammoth character of indeterminate growth or gigantism with other characters of commercial value by crossing Mammoth types with ordinary varieties.

The Maryland Narrowleaf Mammoth has been crossed with a number of pure lines of the more distinct varieties of *Nicotiana tabacum,* including White Burley, Yellow Pryor, Little Oronoco, Connecticut Broadleaf, and the very distinct variety known as *N. Chinensis* (S. P. I., No. 42,355). In all these crosses the Mammoth characteristic behaves as a unit character and is recessive to normal size and normal blossoming habit of the ordinary varieties.

A Maryland Mammoth and a Burley Mammoth, secured as the result of the cross Maryland Mammoth $♀ \times$ White Burley $♂$, have also been crossed with the distinct species, *N. sylvestris* and *N. glutinosa*. In these crosses the $F_1$ plants invariably have blossomed normally as where crosses were made with varieties of *N. tabacum.*

Under normal field conditions, first generation plants of all Mammoth crosses have blossomed in practically the same period required by the ordinary varieties of *N. tabacum*. The plants, however, are usually somewhat taller and, on an average, produce a somewhat higher leaf number than the ordinary varieties, showing that the $F_1$ plants are more or less intermediate between the normal and the Mammoth parents. This relation of leaf number is shown in Table I.

In crosses between Little Dutch and Maryland Mammoth, the $F_1$ plants were also somewhat larger and produced more leaves than the Little Dutch parent. $F_1$

### TABLE I

COMPARISON OF NUMBER OF LEAVES OF $F_1$ PLANTS OF CROSSES BETWEEN MARYLAND MAMMOTH AND NORMAL VARIETIES

| Variety | Leaf Number Classes | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 23 | 25 | 27 | 29 | 31 | 33 | 35 | 37 | 39 | 41 |
| Yellow Pryor................... | 2 | 7 | 1 | | | | | | | |
| Md. Mammoth ♀ × Yellow Pryor ♂ ... | | | 1 | 1 | 1 | 6 | 7 | 2 | 2 | |
| Little Oronoco................... | 1 | 1 | 2 | 3 | 3 | | | | | |
| Md. Mammoth ♀ × Little Oro. ♂...... | | | | | 1 | 3 | 2 | 11 | 4 | 1 |
| White Burley................... | 1 | 4 | | | | | | | | |
| Md. Mammoth ♀ × White Burley ♂ ... | | | | | | 1 | 6 | 10 | 5 | 1 |

plants of the cross Maryland Mammoth ♀ × *N. Chinensis* ♂ (S. P. I., 42,355) were grown in 1918, and records of dates of blooming were made for comparison with the dates of blooming of the parent *N. Chinensis*, which is an unusually small and early maturing variety of *N. tabacum*. From the following table it is evident that the parent *N. Chinensis* blossomed somewhat earlier than the $F_1$ plants of the cross with Maryland Mammoth:

### TABLE II

NUMBER OF DAYS ELAPSING FROM TRANSPLANTING TO DATE OF FIRST BLOOM OF $F_1$ PLANTS OF CROSS MARYLAND MAMMOTH ♀ × N. CHINENSIS ♂ AND PLANTS OF THE PARENT VARIETY OF N. CHINENSIS

| Variety | Classes | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 45 | 47 | 49 | 51 | 53 | 55 | 57 | 59 | 61 | 63 |
| N. Chinensis................... | 8 | 5 | 11 | 2 | 10 | 1 | 6 | 0 | 2 | 5 |
| Md. Mammoth ♀ × N. Chinensis ♂ .... | | | | 1 | 14 | 1 | 14 | 2 | 1 | 11 |

In the cross Maryland Mammoth × White Burley, Mammoth Burley types have consistently appeared in the $F_2$ progenies, and have since remained true to Mammoth character. These have been crossed with a number of different types and varieties of *N. tabacum*. During the summer of 1918 considerable data were secured at Arlington, Va., showing the segregation of plants of Mammoth character in the $F_2$ of many crosses.

Let us first consider the behavior of different Mammoth types when intercrossed. In these lines the Maryland

Mammoth (narrowleaf type) has been crossed with Stewart Cuban (a giant type previously mentioned as originating in Connecticut in Cuban shade-grown tobacco), and also with a Mammoth Burley type, which was secured in the $F_2$ generation of the cross Maryland Mammoth $\times$ White Burley. In the cross Maryland Mammoth $\times$ Stewart Cuban, many plants of the $F_1$ generation were grown, all of which were of Mammoth habit of growth. Selections of these $F_1$ plants were grown and bred true to the Mammoth habit.

In the cross Maryland Mammoth $\female \times$ Burley Mammoth $\male$ many $F_1$ plants were grown at Arlington, Va., in 1918. Of a total of 558 individuals, all were of Mammoth habit and of this number twenty-one were yellowish green like the normal White Burley variety, and 237 were full green in color like the Maryland Mammoth parent.

In a study of the reappearance of Mammoth types in the $F_2$ generation of crosses involving Mammoth and normal forms, several different combinations have been made. In one group both parents were of Burley type. In the second group one of the parents was normal green and the other of Burley type. In the third group both parents were green.

In the first group, involving Burley color in both parents, one of the parents was the Burley Mammoth secured in the $F_2$ generation of the cross Maryland Mammoth $\times$ White Burley. From the cross Mammoth Burley $\female \times$ ordinary White Burley $\male$, 638 $F_2$ plants were grown, of which 158 were Mammoth. This is a very close approximation to the theoretical Mendelian ratio $638/4 = 159.2$, which should obtain in a cross involving two simple contrasted Mendelian characters.

From the cross White Burley type of 30A,[2] $\female \times$ Burley Mammoth $\male$, 348 $F_2$ plants were obtained, of which eighty were of Mammoth habit of growth. This figure closely approximates the theoretical Mendelian ratio $348/4 = 87$.

[2] The type designated as White Burley type of 30A is a tall, vigorous Burley type originally obtained from the cross Connecticut Broadleaf $\times$ White Burley.

Of the total number of Mammoth plants, *i. e.*, 986, appearing in the $F_2$ of these crosses, only two were Green Mammoth, the rest being typically of Burley character. Whether these two exceptions represent mixtures or reversions can not be stated.

In the second group, one of the parents involved in the original cross was Green, the other being of Burley character.

From the cross Connecticut Broadleaf ♀ × Burley Mammoth ♂, 305 $F_2$ plants were grown, of which sixty-nine were of Mammoth habit. This approximates the theoretical ratio $305/4 = 76.2$. From the cross Maryland Mammoth ♀ × White Burley type of 30A ♂, 152 $F_2$ plants were grown, of which forty were of Mammoth habit. This figure is very close to the theoretical ratio $152/4 = 38$. Of the total number of Mammoth plants, *i. e.*, 457, which appeared in the two crosses Connecticut Broadleaf ♀ × Burley Mammoth ♂ and Maryland Mammoth ♀ × White Burley type 30A ♂, only two were of Burley color, the rest being green.

We will now consider the third group, which involves normal green color in both parents.

From the cross Connecticut Broadleaf ♀ × Maryland Mammoth ♂, 175 $F_2$ plants were grown, of which thirty-nine were of Mammoth habit.

From the cross Maryland Mammoth ♀ × Yellow Pryor ♂, eighty-three $F_2$ plants were grown, of which twenty-five were Mammoth.

From the cross Little Dutch ♀ × Maryland Mammoth ♂, 119 $F_2$ plants were grown, of which twenty-eight were Mammoth. A total of 377 plants were grown in these crosses, of which ninety-two were Mammoth plants. This is a very close approximation to the expected ratio $377/4 = 94.2$.

Considering all the crosses in the three groups involving the Mammoth character in one of the parents a total of 1,820 $F_2$ plants were grown, of which 439 were of Mammoth character. This is a fair approximation to the

expected ratio $1820/4 = 455$, if the Mammoth habit behaved as a simple Mendelian character in contrast with the normal blossoming habit.

From these data it would appear that the Mammoth character is recessive in its inheritance and reappears in the $F_2$ generation in numbers approximating closely the expected ratio for a simple Mendelian recessive.

### The Origin and Behavior of a New Mammoth Type of Tobacco in a Line Descending from a Species Hybrid

In an earlier paragraph it has been mentioned that the Maryland Narrowleaf Mammoth and a Burley Mammoth appeared in the $F_2$ generation of certain crosses. In the writer's experience a giant type appeared in third generation plants descending from a species cross.

In 1914 the blossoms of a first generation plant of the cross Connecticut Broadleaf (pink) ♀ × Giant Red flowering (carmine) ♂ were pollinated with the pollen of *Nicotiana sylvestris* (white).[3] Although first generation plants of crosses between the species *N. tabacum* and *N. sylvestris* are likely to be sterile, or nearly so, considerable fertile seed were obtained from $F_1$ generation of this particular cross. In the second generation there was a noticeable segregation into plants with pink, white and carmine blossoms. The size and shape of the blossoms of the plants of the $F_2$ generation were also very variable and various abnormalities were noted. Some plants were completely self-sterile and others produced blossoms with supernumerary petals. A number of plants producing the largest and finest carmine-colored blossoms were selected for further inheritance studies. The progenies of two of these mother plants, nos. 9 and 12, were grown in the field at Arlington, Va., during the season of 1916.

The mother plant, no. 9, proved to be heterozygous, breaking up into carmines and pinks, approximating the theoretical ratio of three carmines to one pink. All the plants of this line were normal in size and habit of growth.

[3] The so-called Giant Red flowering tobacco sold by seedsmen for ornamental purposes, is only a variety of *N. tabacum* with deep carmine blossoms.

The sister plant, no. 12, which proved to be homozygous for carmine, behaved differently, giving rise to a progeny of plants which were very variable in height.[4] A number of these plants appeared to possess the Mammoth habit of indeterminate growth and gave no evidence of blossoming. On October 26, 1916, the heights of the plants, all of which had blossomed except those of Mammoth habit of growth, were as follows:

TABLE III.

HEIGHTS OF THE PLANTS IN THE PROGENY OF SISTER PLANT NO. 12

| | Height classes | | |
|---|---|---|---|
| | 3 to 5 ft. | 5 to 7 ft. | 7 to 9 ft. |
| Number in class.... | 12 (blossomed) | 16 (blossomed) | 3 (Mammoth) |

The shortest plants in this progeny were first to blossom and produced an average of only 20 to 25 leaves, including the first bald sucker. Other plants of intermediate heights blossomed considerably later and produced an average of 35 to 40 leaves, including the first bald sucker. Those plants of Mammoth habit of growth which showed no indications of blossoming had produced considerably more than 40 leaves.

Two of these Mammoth plants, nos. 12 (a) and 12 (b), each seven feet in height, were transplanted in the greenhouse October 21 without cutting them back. Both plants blossomed December 8, producing carmine blossoms. Plant no. 12 (a) had produced 70 to 75 leaves, not including many bract-like leaves below the flowerhead. Plant no. 12 (b) produced 60 to 65 leaves, including all small ones below the flowerhead.

In addition to these two Mammoth plants the seed of several of the taller sister plants, nos. 12 (c) and 12 (d), in class 2, which had blossomed late, producing 35 to 40 leaves, were saved separately. The progenies of all were grown in the field at Arlington Farm, Va., in 1917. A

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[4] The leaves of the mother plant no. 12 were characterized by coarse, thick, broad and rounded blades abruptly contracted at the base to a long, almost naked or slightly winged petiole. This striking type of leaf has remained constant in the progeny of no. 12, and also in the progenies of no. 12 (a), 12 (b), 12 (c) and 12 (d), descending from this mother plant.

total of 60 plants was grown from the Mammoth mother plant, no. 12 (a), all of which were of Mammoth type, with an average height of seven to seven and a half feet. On September 11 a few of the tallest plants were eight feet in height. On this date an average of 50 to 55 leaves had been produced and none showed any evidence of blossoming. A progeny of 60 plants (see row 38A, 1917) was also grown from the Mammoth mother plant, no. 12 (b). On September 11 these plants averaged six and a half to seven feet in height and resembled the progeny of no. 12 (a) in all respects except that they were not quite as tall.

From the mother plant, no. 12 (c), which was one of the late blossoming plants, producing an average of 35 to 40 leaves, 49 plants were grown. On September 13 the heights of 48 of these plants and their blossoming habits were noted as follows:

### TABLE IV

HEIGHTS OF 48 PLANTS IN THE PROGENY OF MOTHER PLANT No. 12 (c) SE-
LECTED FROM CLASS 2, OF TABLE III

| | Height of classes | | | | |
|---|---|---|---|---|---|
| | 5 to 7 ft. | | 7 to 9 ft. | | 1 to 11 ft |
| | Normal | Mamm. | Normal | Mamm. | Normal | Mamm. |
| Number in class .. | 2 | 2 | 20 | 12 | 12 | 0 |

The height of one plant which blossomed was not obtained and is not in-
cluded in the table.

In this progeny of 49 plants it is evident that 14 plants possessed Mammoth characteristics of continuous growth and showed no evidence of blossoming, while 35 plants, some of which were of giant stature, blossomed. From the late blossoming mother plant, no. 12 (d), a progeny of 48 plants was grown. The heights of 42 of these plants were also measured on September 13 and their blossoming habits noted as follows:

### TABLE V

FREQUENCY DISTRIBUTION OF HEIGHTS OF 42 PLANTS IN PROGENY OF MOTHER
PLANT No. 12 (d) SELECTED FROM CLASS 2 OF TABLE III

| | Height of class | | | | | | |
|---|---|---|---|---|---|---|---|
| | 3 to 5 ft. | | 5 to 7 ft. | | 7 to 9 ft | | 9 to 11 ft. |
| | Normal | Mamm. | Normal | Mamm. | Normal | Mamm | Normal | Mamm. |
| Number in class .... | 0 | 1 | 17 | 0 | 19 | 0 | 4 | 1 |

Six other plants were grown in this progeny which are not included in the
table since their heights were not obtained. All blossomed, however.

In addition to these individual progenies of the sister plants, nos. 12 (a), (b), (c) and (d), selected from the progeny of the mother plant, no. 12, in 1916, a mixed lot of seed was harvested from several other sister plants which had blossomed. Fifty-six plants were grown from this mixed lot of seed, all averaging six to six and a half feet in height, and all blossoming. In this lot of plants there were no indications of Mammoth types and so far as could be determined with the eye, no intermediate forms were present.

From the inheritance behavior of the sister plants, nos. 12 (a), (b), (c) and (d), it is evident that pure Mammoth types, breeding true, and intermediate inconstant types appeared simultaneously in the progeny of the original mother plant, no. 12. These intermediate plants behaved as hybrid forms, in that they gave rise in their progeny to a certain percentage of typical Mammoth, non-blossoming types. Since the progenies of the two sister plants, nos. 12 (c) and (d), were handled under similar conditions from the time the seed were sown, it is evident that the mother plant, no. 12 (c), yielding 14 Mammoth plants in a total of 49 plants, was considerably more prolific in Mammoth individuals than the sister plant, no. 12 (d), which yielded only two Mammoth individuals in a total of 48 plants.

It is of interest to note that Lodewijks (1911) in working with tobacco in Java, has observed the occurrence of Mammoth types which breed true and also intermediate or inconstant races which break up into Mammoth or Giant forms approximating the theoretical Mendelian ratio of 25 per cent.

Lodewijks regards these inconstant races as hybrid mutations and states the results of his investigations as follows, a translation of which will also be given:

### Translation

I. Occasionally giant plants which breed true to type occur in Vorstenland tobacco.

II. Evidently giant intermediate races also occur.

III. In my experiments I obtained either an atavist of an inconstant intermediate race or a hybrid-giant.

IV. As none of the giant plants in my experiments have reached the flowering stage, it is not certain which of the two mentioned possibilities is the chief. It would seem to be the latter, however, as seed of the few-leaved mother plant of the second generation produced exclusively plants while seed of the many-leaved plant produced nearly 25% giant and many-leaved and few-leaved plants.

V. It is probable, therefore, that a second instance is present of a mutation arising as a hybrid.

Honing (1914), in his studies of the aberrant types occurring in Sumatra and Java tobacco, states that in some instances 100 per cent. of the progeny of normal plants were of the Mammoth type. According to Honing even the Mammoth plants were not always constant in their inheritance, and intermediate races were also present.

From Lodewijk's observations in Java, and the writer's observations at Arlington Farm, Va., it is evident that intermediate races, as well as Mammoth types which breed true, may appear in a progeny. Concerning the actual mode of origin of these intermediate and Mammoth races nothing definite is known. Hayes and Beinhart (1914), speaking of the origin of a Mammoth Cuban type in Connecticut in 1912, say:

This mutation must have taken place after fertilization, *i. e.*, after the union of the male and female reproductive cells. If the mutation had taken place in either the male or female cell before fertilization, the mutant would have been a first generation hybrid, and would have given a variable progeny the following season.

They assume that if one gamete alone were affected, a progeny of hybrid character would have resulted, but if we assume that one gamete can become so affected, it is quite as reasonable to assume that both may sometime be changed in the same manner. If such were the case, Mammoth plants breeding true to this indeterminate habit of growth would be expected. .

If, as Lodewijk finds, intermediate races behave as true Mendelian hybrids, producing the theoretical ratio of 25

per cent. true Mammoth plants which breed true, there is strong reason to believe that the change responsible for Mammoth habit of growth has affected one gamete only. If this gamete unites with a normal gamete, then the simple Mendelian ratio would follow, just as in the case of an artificial cross between gametes produced by a Mammoth plant and those of a normal plant. In the one case a portion or all the gametes bearing the Mammoth character are produced by a normal plant. In the other case, Mammoth plants themselves produce gametes with potential Mammoth characters. In the experience of Honing, normal plants have even produced progenies containing 100 per cent. mammoth plants. This behavior would indicate that all the gametes produced by a mother plant may sometimes become modified to express the Mammoth habit of growth. Although Honing has observed the complete disappearance of a line of Mammoth plants which gave rise to progenies of blossoming plants, this behavior has not been definitely observed in this country except as a response to obscure environmental conditions. It is possible that the behavior of Honing's inconstant Mammoths is of this nature rather than an internal gametic change, permanently affecting the heredity of the Mammoth feature. Until this question is more definitely settled, Honing's inconstant Mammoth can not be disposed of.

Since inconstant, intermediate plants behaving as Mendelian hybrids with respect to Mammoth character, and sister plants of pure type are known to arise suddenly in the same progeny, there is reason to believe that the change responsible for Mammoth behavior may affect one or both gametes, as the case may be. This inconstant behavior of these mutant hybrids is particularly significant since it appears in every way similar to the actual behavior of a controlled cross between a Mammoth and a normal plant. Of course, if it is possible for one or more gametes produced by a normal plant to become so modified as to originate a hybrid-mutant or a pure line mutant,

then it is quite as probable that all the gametes in a single blossom, or the gametes produced by all the blossoms of a normal plant, may become so modified. Honing's observations at least would indicate that this does occur.

In those instances where an occasional Mammoth appears in the progeny of a normal plant, it is usually assumed that the change responsible for the Mammoth character was associated in some way directly with the gametes themselves. In those instances where many or even all the plants in the progeny of a normal plant produce Mammoths, the question becomes more involved and difficult of interpretation. It is very difficult to see how all the gametes of a normal plant can become simultaneously modified to produce by their union Mammoth plants, unless we assume that the change takes place at some stage preceding the development of the gametes. Should the change take place in a mother cell of the anther preceding tetrad formation, *i. e.*, by the addition or subtraction of some factor in the chromosome material, it is reasonable to suppose that the four pollen grains resulting from the division of this mother cell may be similarly affected, and bear the Mammoth character. It is possible, however, that the change may take place very much earlier, so that a part or even all the sporogenous cells will be affected. If this condition occurred, it is easy to see how great numbers or even all the pollen grains arising from their division would bear the Mammoth character. Since the development of the megasporangium is in every way parallel to the development of the microsporangium or anther, similar changes would affect one or more egg-cells, depending upon whether the change responsible for Mammoth character took place immediately in the egg-cell itself, in the mother cells, or very much earlier, so that all the sporogenous cells, and hence all the egg-cells arising from them, are affected. Such changes affecting great numbers or all the gametes in a single flower, or even in the entire flower head itself, would produce the phenomenon of a more or less complete acquirement of Mam-

moth character in the progeny of a normal plant.  It may
be stated here that East (1917) has offered the same sug-
gestion concerning the origin of variations in cell-divi-
sions preceding the formation of the gametes themselves.

### The Production of New Mammoth Forms by Hybridization

Two Mammoth types of tobacco are now grown com-
mercially in the United States, the Maryland Narrowleaf
Mammoth in Maryland, and to a lesser extent the Stew-
art Cuban in the Connecticut Valley.  Promising Mam-
moth types have also originated in Havana Seed tobacco
in Connecticut.  Beinhart (1918, however, in a brief dis-
cussion of the occurrence of Mammoth types in the Con-
necticut Valley, states that practical methods of seed pro-
duction and special cultural methods must be worked out
before the Stewart Cuban Mammoth and the Havana Seed
Mammoth can be successfully grown on a commercial
scale.  Although these Mammoths originated spontane-
ously from commercial types, there is every reason to
believe that valuable new types can be secured by cross-
ing with the ordinary commercial types of tobacco.
Since in crosses with ordinary varieties gigantism is re-
cessive in its inheritance, the problem of producing new
giant types by hybridization and recombination has not
been difficult.  Several Mammoth types have already
been secured in crosses with Connecticut Broadleaf, Little
Dutch and White Burley.  If by this means it is possible
to combine the habit of gigantism, which insures greatly
increased yields, with the desirable quality characteris-
tics of ordinary varieties, very valuable commercial types
can be obtained.

### Summary

1. Gigantism has occurred in several different commer-
cial varieties of tobacco, including Maryland types, Cu-
ban, Connecticut Havana and Sumatra.  It has also been
associated with certain varietal crosses and species
crosses.

2. Not only giant or mammoth types which breed true, but intermediate or hybrid types occur spontaneously which subsequently give rise to a greater or less proportion of mammoth forms.

3. In crosses with normal varieties the mammoth character is recessive, and $F_1$ plants invariably blossom. The $F_1$ plants average a somewhat higher leaf number than the normal parent which entered into the cross.

4. In the $F_2$ generation mammoth plants occur in proportions approaching the theoretical ratio of 25 per cent. obtaining in a single Mendelian cross involving two contrasted unit characters.

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# THE MENDELIAN BEHAVIOR OF AUREA CHAR-ACTER IN A CROSS BETWEEN TWO VARIETIES OF NICOTIANA RUSTICA

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## INTRODUCTION

THE species of tobacco *Nicotiana rustica* comprises a number of more or less distinct varieties. One of the more characteristic varieties which was received from Russia (S. P. I. 35080) is a light, yellowish-green type with distinctly white stems and midribs. In these respects this type of *N. rustica* resembles the well-known White Burley variety of *N. tabacum*. According to Splendore,[1] who has described it in detail, this white-stemmed variety of *N. rustica* is grown commercially in Russia (Makorka, Bakoun, Kolmak, Tseco, etc.) as a pipe and cigarette tobacco. In this variety of *N. rustica,* the stems of young plants—especially if they have been somewhat etiolated by crowding—are almost snow white. A cross section of the stems of such plants one month old reveals the fact that this whiteness is not merely superficial, but extends entirely through the stems, whereas in green varieties of *N. rustica* the internal structure of the stems is green throughout. The cotyledons are decidedly chlorotic and the leaves have a pale yellowish-green, chlorotic appearance which becomes more marked as the plants approach maturity. As a matter of convenience, the writer has applied the term "aurea" to this peculiar, varietal form of chlorosis.[2]

[1] Splendore, A., "Due Particolore Forme Di N. Rustica Brasilia Chwitzent e Kapa Magiara," *Boll. Tech. Della Colt. Dei Tabachi del R. Inst. sperimentale, Scafati* (Salerno), XI, No. 2, 1912.

[2] This type of *aurea* appears to be quite distinct from the type of *aurea* described by Lodewijks as having occurred suddenly in plants of *N. taba-*

### DOMINANCE OF GREEN PLANT COLOR IN $F^1$ PLANTS OF CROSSES

In 1914 the writer made reciprocal crosses of this white-stemmed, chlorotic *aurea* type of *N. rustica,* with green-stemmed, green-leaved type, and several hundred $F^1$ plants were grown in the field at Arlington, Va., during the season of 1915. All the $F^1$ plants were green in color, whichever type was used as the seed-bearing parent. It was at once evident that the white-stemmed, chlorotic, *aurea* character behaved as a simple recessive to normal greenness of stem and leaf. To determine more fully the Mendelian behavior of this cross an analysis of the $F^2$ and $F^3$ generations was made.

### SEGREGATION IN $F^2$ PLANTS

In the $F^2$ generation, green- and white-stemmed *aurea* plants appeared. So distinct is the white-stemmed recessive that four or five weeks after germination, the young plants can be readily distinguished from the green-stemmed types. This made the growing and handling of large numbers of plants a comparatively easy matter, since it was only necessary to grow them to the size of small seedlings and obtain counts when they were four or five weeks old. In the following table an analysis of 25,000 $F^1$ plants is shown.

From this data it is evident that the recessive white-stemmed *aurea* type of *rustica* appeared in numbers approximating very closely the theoretical Mendelian ratio of 25 per cent., since in a population of 25,000 plants, 24.31 per cent. were of the white-stemmed, *aurea* type.

*cum* in Java. He found that this type of *aurea* was inconstant in its inheritance, since *aurea* mother plants always gave progenies consisting of green and *aurea* plants. In crosses between *aurea* and green plants the $F^1$ generation always included *aurea* and green plants. From the inconstant inheritance of this character he concludes that this *aurea* form originated as a mutant with an essentially hybrid constitution. See Lodewijks, J. A., "Erblichkeitsversuche mit Tabak," *Zeitschr. für Induktive Abstammungs. Vererbungslehre,* Vol. 5, 1911, pp. 139–172.

TABLE I

RATIOS OF GREEN-STEMMED AND RECESSIVE WHITE-STEMMED AUREA PLANTS
IN THE F$^1$ GENERATION OF THE CROSS 35080 (WHITE-STEMMED)
♀ × No. 1 FROM INDIA (GREEN-STEMMED) ♂

| Date of Count | Total Number Counted | Number of Green-stemmed | Number of White-stemmed *aurea* | Percent. of White-stemmed *aurea* |
|---|---|---|---|---|
| June 19, 1918 | 4,188 | 3,178 | 1,010 | 24.1 |
| May 16, 1918 | 1,167 | 887 | 280 | 23.9 |
| May 17, 1918 | 417 | 308 | 109 | 24.9 |
| June 24, 1918 | 1,955 | 1,476 | 479 | 24.5 |
| June 25, 1918 | 279 | 231 | 48 | 17.2 |
| July 1, 1918 | 1,072 | 818 | 254 | 23.6 |
| July 16, 1918 | 747 | 594 | 153 | 20.4 |
| July 18, 1918 | 1,246 | 930 | 316 | 25.3 |
| Sept. 3, 1918 | 2,114 | 1,597 | 517 | 24.4 |
| Oct. 18, 1918 | 2,253 | 1,707 | 546 | 24.2 |
| Oct. 21, 1918 | 2,673 | 2,035 | 638 | 23.8 |
| Oct. 24, 1918 | 4,556 | 3,400 | 1,156 | 25.3 |
| Oct. 26, 1918 | 2,333 | 1,760 | 573 | 24.5 |
| Totals | 25,000 | 18,921 | 6.079 | 24.31 |

## BEHAVIOR OF F$^2$ GREEN PLANTS AND WHITE-STEMMED EXTRACTED *aurea* RECESSIVE

Of twenty-eight F$^2$ green plants selected at random the character of the inheritance in the progenies of those showing segregation was noted as follows:

TABLE II

RATIOS OF GREEN-STEMMED AND WHITE-STEMMED AUREA PLANTS APPEARING
IN THE PROGENIES OF HETEROZYGOUS GREEN-STEMMED PLANTS IN
THE F$^2$ GENERATION

| Number of Mother Plant | Total Number of Progeny Counted | Number of Green-stemmed Plants | Number of White-stemmed *aurea* Plants |
|---|---|---|---|
| 1 | 414 | 300 | 114 |
| 4 | 401 | 300 | 101 |
| 5 | 462 | 345 | 117 |
| 6 | 392 | 300 | 92 |
| 7 | 887 | 649 | 238 |
| 10 | 403 | 304 | 99 |
| 11 | 395 | 300 | 95 |
| 12 | 386 | 300 | 86 |
| 14 | 399 | 300 | 99 |
| 17 | 390 | 300 | 90 |
| 21 | 410 | 310 | 100 |
| 23 | 397 | 300 | 97 |
| 24 | 660 | 503 | 157 |
| 27 | 995 | 747 | 248 |
| 28 | 739 | 561 | 178 |
| 33 | 393 | 300 | 93 |
| Totals | 8,123 | 6,119 | 2,004 |

The green $F^2$ individuals Nos. 2, 3, 9, 13, 15, 16, 18, 19, 20, 25, 29, 30 were homozygous for greenness and gave pure green progenies. A progeny of several thousand plants was grown from each individual.

Of 8,123 plants descending from heterozygous green individuals analyzed in Table II, 2,004 or 24.6 per cent. were white-stemmed recessives. It is evident that these figures for the extracted recessives also approach very closely the theoretical 25 per cent. Mendelian ratio which obtains for contrasted characters in simple hybrids. This ratio of 24.6 per cent. extracted recessives of the *aurea* type descending from green heterozygous $F^2$ individuals, is very close to the ratio 24.3 per cent. obtained in a count of 25,000 individuals descending from $F^1$ plants. Since 12 of the 28 green $F^2$ plants tested were homozygous for greenness and gave all green progenies, it is evident that these were extracted dominants.

The progenies of 20 extracted white-stemmed *aurea* recessives of the $F^2$ generation were also studied. Several thousand plants were grown from each of the 20 individuals, and all proved homozygous for the *aurea* character, etc.

### Behavior of Back Crosses

First generation plants of the original cross No. 35080 (white-stemmed *aurea*) ♀ × No. 1 from India (green-stemmed *Rustica*) ♂ were now crossed with the parent green-stemmed and white-stemmed *aurea* types.

In the back cross with the recessive white-stemmed *aurea* parent 591 plants were obtained of which 303 were green-stemmed individuals, and 288 were *aurea*. These figures approach the theoretical 1 : 1 ratio which may be expected in such crosses.

In the back cross with the dominant green-stemmed type, 280 plants were obtained, all of which were green-stemmed.

From these results obtained with the cross between the green-stemmed types of *N. rustica* and the distinctive

white-stemmed *aurea* type, it is evident that we are dealing with a clear-cut instance of Mendelian behavior, in which greenness of stem and leaf is contrasted with the character of white stems and a yellowish, chlorotic appearance of the leaves. Since these characteristics are readily distinguished in plants in the seedling stage, only five or six weeks after germination, this cross is especially favorable for the demonstration of simple Mendelian behavior in all its phases. The technique of crossing is simple, and many thousands of seedlings may be grown in a comparatively small area in a short time.

## Summary

In crosses between a distinctive white-stemmed *aurea* type and green-stemmed type of *N. rustica* the following Mendelian relations were found:

In $F^1$ plants the white-stemmed *aurea* type is recessive to the green-stemmed type.

$F^2$ plants segregate into green-stemmed and white-stemmed *aurea* plants. Approximately 25 per cent. of the plants are *aurea* recessive. Some of the green plants are homozygous for greenness of stems, etc., and some are heterozygous, again segregating into green and white-stemmed *aurea* types with the same ratios obtained in the $F^1$ generation. The extracted *aurea* recessives of the $F^2$ generation are homozygous with respect to the character of white stems, etc., peculiar to this type.

In back crosses between a heterozygous $F^1$ plant and the dominant green-stemmed type, the progeny consists of 100 per cent. green-stemmed plants.

In back crosses with the recessive *aurea* type, the progeny consists of green-stemmed and white-stemmed *aurea* plants in approximately the expected ratio of 1 to 1.

# SOME FACTOR RELATIONS IN MAIZE WITH REFERENCE TO LINKAGE

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In view of the many distinct Mendelizing characters known in maize (*Zea mays* L.) it has been rather surprising that so few cases of linkage have been reported in this plant up to the present time. The number of chromosome pairs, about ten, is not large for plants and about twenty distinct contrasting factors are known of which the inheritance can be easily followed and about as many more which offer some difficulty in following in transmission but which can be used more or less satisfactorily in carrying on experiments on linkage. The writers have made no systematic search for cases of linkage in maize, but having found, almost accidentally, what seems to be a fairly good case of linkage between the tunicate factor which determines the production or inhibition of the glumes covering the seeds and the factor for starchy or sweet endosperm, the results are reported here in the hope that they may be of use to others who may be pursuing investigations along this line.

Collins and Kempton (1911) were the first to record a case of linkage in maize. Their results involved the relation of endosperm texture, as contrasted in our ordinary starchy varieties with the waxy condition found in Chinese varieties, to the color of the aleurone layer. They did not determine which of the several factors concerned with aleurone color was involved in this linkage. More recently Bregger (1918) has given additional proof of this case of linkage. He has determined the amount of crossing-over and has also shown that it is the C aleurone factor (East and Hayes, 1911; Emerson, 1918) which is the one involved. At about the same time Lindstrom (1917) reported the second case of linkage, that of one of

the factors of chlorophyll color G, with another aleurone
color factor, this time the R factor, which in the presence
of a suitable basic factorial combination produces red
color in the aleurone cells.    More recently Lindstrom
(1918) has found another chlorophyll factor L linked with
R and G.    L is completely linked with R and both show
about the same amount of breaks in the linkage with G.
This makes the first group of three factors so far reported
in maize.

### Linkage between Tunicate Ear and Starchy-Sweet Endosperm Factors

The curious type of maize, known generally in this
country as pod corn (*Zea mays tunicata* Sturtevant) is
considered by Collins (1917) not to be a pure type, but a
heterozygous condition somewhat analogous to the blue
Andalusian fowl.    When selfed seed of the typical podded
ears are planted Collins finds that three types of plants
are produced: one type like the typical podded parent;
one with normal ears without the enclosing glumes; and
one anomalous type of a plant which does not produce
seed in lateral inflorescences, but in perfect flowers in the
tassels.    On these last plants lateral inflorescences with
much elongated glumes are produced, but are sterile.    All
these three types have been secured in about the ratio of
1:2:1 as expected on the assumption that a single Men-
delizing difference is involved and the heterozygote is
distinguishable from both homozygotes.

Our own rather limited experience with this type of
maize confirms Collins's conclusions.    In 1915 seed of a
typical podded ear was planted (there was no record
whether it had been selfed or not).    All three types which
Collins described later were obtained.    A number of typi-
cal podded plants were self-pollinated and grown the
next year in the hope of getting a pure podded strain.    At
that time no thought was given to the possibility of its
being a heterozygous type.    The plants with seeds in the
tassels were thought to be extreme variations from the

usual type. Nine selfed ears were obtained and grown the following year and all gave some plants with podless ears and others with seeds in the tassels as well as plants of the typical pod type. No record was made of the numbers in each class, but it was noted as rather surprising that all of the nine ears gave some normal non-pod plants.

An attempt was made to self-pollinate some of the plants with the peculiar terminal inflorescences which were easily recognized as the type which produced seed, but no seed was obtained where they were enclosed in a bag. Very little good pollen is produced in these tassels and probably all or most of the seeds which are produced on open-pollinated plants result from crossing with foreign pollen. One tassel with a number of such open-pollinated seeds was saved and the seed planted. No normal non-pod ears were obtained. Most of the ears were of the typical pod type or half-tunicate as named by Collins. All of these results bear out the assumption of Collins that the podded maize considered by Sturtevant (1899) as a separate species and stated by him to have been known for 300 years is not a constant type and has little more claim to specific rank than the blue Andalusian fowl.

One of the half-tunicate ears produced from the open-pollinated seed of the perfect flowered segregate was self-pollinated, and when examined this ear was found to have segregated into starchy and sweet seeds, showing that the plant which had furnished the pollen had sweet seeds. Since all the podded maize which had been grown up to that time was starchy and all of the sweet maize was non-podded, the cross involved the tunicate character and starchy endosperm from the female parent, and non-tunicate, sweet endosperm from the male. The starchy and sweet seeds were planted separately. There were 173 of the starchy and forty-three of the sweet seeds. Not a perfect 3:1 ratio, but reasonably close. All of the seeds were planted, but since not all of each type produced a mature plant, it is legitimate to correct the observed re-

sults according to the theoretical starchy-sweet ratio.
The results obtained and corrected in this way are as
follows:

| | Starchy Tunicate | Starchy Non-tunicate | Sweet Tunicate | Sweet Non-tunicate |
|---|---|---|---|---|
| Found. .............. | 113 | 4 | 7 | 25 |
| Corrected ............ <br> Starchy-sweet ratio | 108.0 | 3.8 | 8.2 | 29.1 |
| Expected. ............ <br> 11:1:1:11 gametic ratio | 105.8 | 6.0 | 6.0 | 31.3 |

The numbers are small, but the distribution obtained is
clearly different from a 9:3:3:1 ratio. The agreement
with the nearest theoretical results, assuming linkage, is
close ($P = .615$). The per cent. of crossing-over, 8.3, in-
dicated by these figures is low. In the other cases of
linkage reported, the percentages of crossing-over were
much higher, 25.7 per cent. in the waxy endosperm-
aleurone color combinations and 20 per cent. in the
aleurone color-chlorophyll color combination with the
exception of the one case where complete linkage has so
far been found.

In making the classification all of the plants which
showed the tunicate character, whether of the half-tuni-
cate or full-tunicate type, were classed as tunicate, as con-
trasted to the normal plants. Segregation was clear be-
tween these two classes and there was little possibility of
confusion even when the ears were immature. On the
other hand, it was not always easy to distinguish full-
tunicate from half-tunicate plants, as the tassels of the
former class do not always produce seed, and the ears,
which are quite characteristic when fully developed, are
not so distinct when immature, and many of these plants
were late in maturing. Any error of classification here
does not affect the linkage results, however. There is one
source of error in that the plants suckered profusely;
many of these bore ears and tassels and were difficult to
distinguish from the main stalk. The plants were grown
in hills, and when classifying them it was not always pos-

sible to tell which was plant and which was sucker, so that the same plants may have been included in the count more than once.

The figures for the segregation with respect to the tunicate character together with the figures from a similar ear, which instead of segregating starchy and sweet segregated for yellow and white endosperm, are given as follows:

|  |  | Normal | Half-tunicate | Full-tunicate |
|---|---|---|---|---|
| Ear 1 | Sweet | 25 | 6 | 1 |
|  | Starchy | 4 | 70 | 43 |
| Ear 2 | White | 10 | 19 | 14 |
|  | Yellow | 36 | 58 | 29 |
| Found | | 75 | 153 | 87 |
| Expected 1:2:1 ratio | | 79 | 158 | 79 |

With regard to this second ear, which was similar to the first except that it was crossed with yellow, starchy, non-tunicate instead of white, sweet maize, it is to be noted that there is no indication of linkage between the factors for tunicate ear and yellow endosperm. The figures obtained compared to the expectancy are given herewith:

|  | Yellow Tunicate | Yellow Non-tunicate | White Tunicate | White Non-tunicate |
|---|---|---|---|---|
| Found | 87 | 36 | 33 | 10 |
| Corrected Yellow-white ratio | 88.1 | 36.4 | 31.9 | 9.7 |
| Expected 9:3:3:1 ratio $P = .739$ | 93.4 | 31.1 | 31.1 | 10.4 |

## Evidence for Linkage between Aleurone Color Factors

Another case of linkage is suggested by the results of East and Hayes (1911) in the inheritance of aleurone color. From crosses of colorless aleurone by purple they obtained marked deviations from the expected ratios which they could not account for. At that time the first

cases of gametic coupling had just been published by Bateson and Punnett and the subject of linkage was not well understood nor its true significance realized. These writers considered the possibility of gametic coupling as a disturbing factor, but came to the conclusion that this phenomenon could not be concerned in their aberrant results.

One of the crosses studied involved two aleurone factors, the basic color factor C and the factor P (Emerson's Pr factor), with R present coming from both parents. This cross was expected to give a ratio of 9 purples : 3 red : 4 non-colored, but actually showed a large excess of purples and deficiency of reds. East and Hayes considered the possibility of linkage between the P and R factors, but since R, according to their theory, was homozygous, crossing-over between these two factors would make no visible difference in the $F_2$ results. On the other hand, since PC entered the cross from one side and pc from the other, the cross-over class pC, if there is linkage, would be red because of the presence of R. Hence any possibility of linkage should be looked for between the P and C factors. Such a situation would account for an excess of purples and a deficiency of reds in the cross under consideration. Another cross involving, in addition to the P and C factors, a color inhibiting factor likewise showed an excess of purples and a deficiency of reds.

Since it is always rather difficult to prove linkage from $F_2$ distributions alone, in this case it would be even more difficult because only one of the cross-over classes, if such it is, can be distinguished. The data of East and Hayes, as far as numbers go, do not agree with expectation from linkage with any amount of crossing-over, and since other crosses involving the same factors have been reported which seem to show independence, it is doubtful whether or not linkage really exists in respect to these two factors. It is more probable that the deviations from theory are to be looked for in either incomplete analysis of the factor relations or faulty classification of the seeds. Red seeds

gradate somewhat into purple and there may be a tendency to include reds among purples. If this were the case, however, wrongly classified purple seeds should sometimes give all red progeny or red and white progeny in the next generation. East and Hayes found no cases of this kind. The possibility of linkage between the P and C factors should be kept in mind until this point can be definitely settled.

## OTHER FACTORIAL RELATIONS

Looking over East and Hayes's data for other cases of linkage or independence of factors there seems to be good evidence that the C aleurone and R aleurone factors are not linked, and also that the factor for sweet endosperm is not linked with either the R or P aleurone factors. In a factorial analysis of the characters of an organism with reference to linkage it is just as important to know the cases where no linkage is shown as those cases where it is shown. Collins and Kempton (1913) give data which indicate independence between sweet and waxy endosperm factors and in another paper (1917) independence between the *tunicata* and *ramosa* factors. East (1910) gives data which indicate that the two factors for yellow endosperm color are not linked with each other and it is quite probable that both of them are independent of the factor for sweet endosperm.

With this evidence we can attempt a beginning at an analysis of the factorial relations in maize. Three independent groups of factors can be tentatively proposed as follows:

| Group I | Group II | Group III |
|---------|----------|-----------|
| Ww Endosperm | Gg Chlorophyll | Ss Endosperm |
| Cc Aleurone | Ll Chlorophyll | Tt Tunicate |
| Pp Aleurone (?) | Rr Aleurone | |

The fact of no linkage between the Cc aleurone and the Rr aleurone color factors separates groups I and II. No linkage between Ww and Ss endosperm factors separates

groups I and III.  No linkage between the Ss endosperm and Rr aleurone factors separate groups II and III.

Since the number of known factor differences in maize is already some three or four times the number of chromosomes, more definite knowledge of the behavior of all these factors in relation to each other will be awaited with interest.  Especially since maize is one of the best materials from the plant side to which the chromosome hypothesis, as worked out in Drosophila, can look for contradiction or support.

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# HOOKE'S MICROGRAPHIA

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BIOLOGICAL research in general during the latter part of the seventeenth century begins to be permeated with an attention to details and with an intensive critical analysis which is conspicuous by its absence in practically all but the masterpieces of previous times. Nor is the explanation far to seek. The improvement of simple lenses and the invention of the compound microscope provided a method of increasing the apparent size of things which, in addition to revealing a new world of "animalcules" beyond the range of unaided vision, brought to the attention of students finer details of structure of the higher animals and plants. But, as Sachs has emphasized, the use of magnifying glasses contributed an advantage of still another kind—it taught those who employed them to see scientifically and exactly. In equipping the eye with increased powers the attention was concentrated on definite points and observation had to be accompanied by conscious critical reflection in order to make the object, which is observed in part only by the microscope, clear to the mental eye in all the relations of the parts to each other and to the whole. Therefore, in marked contrast with the very slow progress in obtaining a mental mastery over the macroscopic morphological features of plants and animals is the work of the early students with the microscope such as Hooke and Grew in England, Malpighi in Italy, and Swammerdam and Leeuwenhoek in Holland.

The earliest clear appreciation of the importance of studying nature with instruments which increase the powers of the senses in general and the vision in particular, is found in a remarkable book by a remarkable

man—the ''Micrographia'' of Robert Hooke, published by the Royal Society of London in 1665 (cf. Fig. 1). The point of view of the author is well illustrated in the following extracts from the preface:

*It is the great prerogative of Mankind above other Creatures, that we are not only able to* behold *the works of Nature, or barely to* sustein *our lives by them, but we have also the power of* considering, comparing, altering, assisting, *and* improving *them to various uses. And as this is the peculiar priviledge of humane Nature in general, so it is capable of being so far advanced by the helps of Art, and Experience, as to make some Men excel others in their Observations, and Deductions, almost as much as they do Beasts. By the addition of such* artificial Instruments



# MICROGRAPHIA:

### OR SOME

*Phyſiological Deſcriptions*

#### OF

## MINUTE BODIES

#### MADE BY

### MAGNIFYING GLASSES.

#### WITH

Obſervations and Inquiries thereupon.

By *R. HOOKE,* Fellow of the Royal Society.

*Non poſſis oculo quantum contendere Lincens,
Non tamen idcirco contemnas Lippus inungi.* Horat. Ep. lib. 1.

*LONDON,* Printed by *Jo. Martyn,* and *Ja. Alleſtry,* Printers to the Royal Society, and are to be ſold at their Shop at the Bell in S. Paul's Church-yard. M DC LX V.

Fig. 1.

*and* methods, *there may be, in some manner, a reparation made for the mischiefs, and imperfection, mankind has drawn upon it self, by negligence, and intemperance, and a wilful and superstitious deserting the Prescripts and Rules of Nature, whereby every man, both from a deriv'd corruption, innate and born with him, and from his breeding and converse with men, is very subject to slip into all sorts of errors.*

*The next care to be taken, in respect of the Senses, is a supplying of their infirmities with Instruments, and, as it were, the adding of artificial Organs to the natural; this in one of them has been of late years accomplisht with prodigious benefit to all sorts of useful knowledge, by the invention of Optical Glasses. By the means of Telescopes, there is nothing so far distant but may be represented to our view; and by the help of Microscopes, there is nothing so small, as to escape our inquiry; hence there is a new visible World discovered to the understanding. By this means the Heavens are open'd, and a vast number of new Stars, and new Motions, and new Productions appear in them, to which all the antient Astronomers were utterly Strangers. By this the Earth it self, which lyes so neer us, under our feet, shews quite a new thing to us, and in every little particle of its matter, we now behold almost as great a variety of Creatures, as we were able before to reckon up in the whole Universe it self.*

*It seems not improbable, but that by these helps the subtilty of the composition of Bodies, the structure of their parts, the various texture of their matter, the instruments and manner of their inward motions, and all the other possible appearances of things, may come to be more fully discovered; all which the antient Peripateticks were content to*
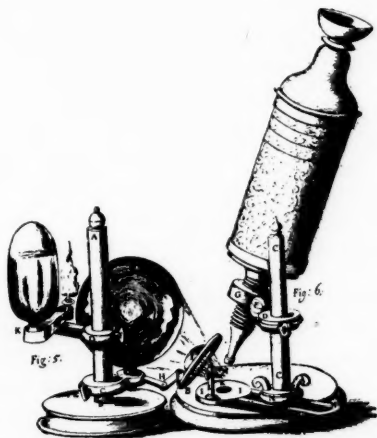


FIG. 2.

*comprehend in two general and (unless further explain'd) useless words of Matter and Form. From whence there may arise many admirable advantages, towards the increase of the Operative, and the Mechanick Knowledge, to which this Age seems so much inclined, because we may perhaps be inabled to discern all the secret workings of Nature, almost*

*in the same manner as we do those that are the productions of Art, and are manag'd by Wheels, and Engines, and Springs, that were devised by humane Wit.*

*In this kind I here present to the World my imperfect Indeavours; which though they shall prove no other way considerable, yet, I hope, they may be in some measure useful to the main Design of a reformation in Philosophy. . . . .*

*As for my part, I have obtained my end, if these my small Labours shall be thought fit to take up some place in the large stock of natural Observations, which so many hands are busie in providing. If I have contributed the meanest foundations whereon others may raise nobler Superstructures, I am abundantly satisfied; and all my ambition is, that I may serve to the great Philosophers of this Age, as the makers and the grinders of my Glasses did to me; that I may prepare and furnish them with some Materials, which they may afterwards order and manage with better skill, and to far greater advantage.*

*Toward the prosecution of this method in Physical Inquiries, I have here and there gleaned up an handful of Observations, in the collection of most of which I made use of Microscopes, and some other Glasses and Instruments that improve the sense; which way I have herein taken, not that there are not multitudes of useful and pleasant Observables, yet uncollected, obvious enough without helps of Art, but only to promote the use of Mechanical helps for the Senses, both in the surveying the already visible World, and for the discovery of many others hitherto unknown, and to make us, with the great Conqueror, to be affected that we have not yet overcome one World when there are so many others to be discovered, every considerable improvemnt of Telescopes or Microscopes producing new Worlds and Terra-Incognita's to our view.*

The author of this work was a versatile genius who applied his powers to a wide field of endeavor—physics, chemistry, mathematics, mechanics, architecture and philosophy—fields which long since have expanded beyond the grasp of one man, and which, even in his own time and by himself, might more profitably have been coped with singly. It is impossible to adequately survey Hooke's varied career within the limits imposed by this paper, but the following extracts from his biography, appended by Richard Waller to Hooke's "Posthumous Works," show what manner of man he was (cf. Fig. 5).

Dr. *Robert Hooke* was Born at *Freshwater,* a Peninsula on the West side of the Isle of *Wight,* on the eighteenth of *July,* being *Saturday,* 1635, at twelve a Clock at Noon, and Christened the twenty sixth following by his own Father Minister of that Parish.

*Schem:XL*

Fig:1.
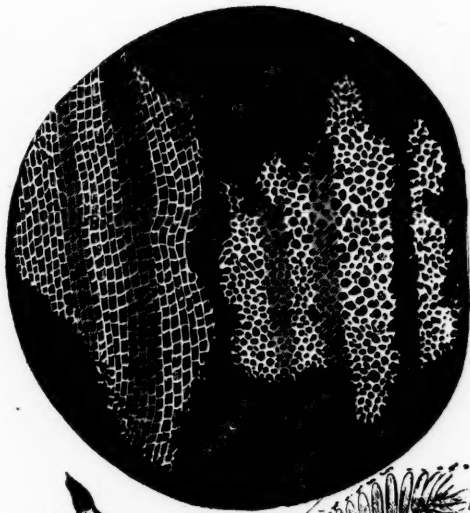


Fig: 2.

FIG. 3.

From *Westminster-School* he went to the University of *Oxford,* in 1653. but as 'tis often the Fate of Persons great in Learning to be small in other Circumstances, his were but mean. I find that he was a Student of *Christ-Church,* tho' not of the Foundation, but was, as I have heard, a Servitor of one Mr. *Goodman,* and took his Degree of *Master of Arts* several Years after, about 1662, or 1663.

About the Year 1655, he began to shew himself to the World, and that he had not spent his Juvenile Years in vain; for there being a Concourse at that time of extraordinary Persons at *Oxford,* each of which afterwards were particularly distinguish'd for the great Light

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some other caverns another, and others in a different Earth, or fish place, for many differing substances have I found in one of these; *several* Shells, and perhaps all their differing from the encompasing earth or stone; the means how all which varieties may be caused, I think, will not be difficult to conceive, to any one that has taken notice of those Shells, which are accidentally found in the perpendent means; which, the thoughts may examine several kinds of such curiously found stones will (I am very apt to think) find reason to ascribe their generation or formation to be ascribable to some such accidents as I have mention'd, and not to any *Plastick virtue*. For it seems to me quite contrary to the infinite prudence of Nature, which is observable in all its works and productions, to design every thing to a determinate end, and for the attaining of that end, makes use of such ways as are (as far as the knowledge of man has yet been able to reach) altogether consonant, and most agreeable to man's reason, and of no way or means that does contradict, or is contrary to humane Ratiocination; whence I have a general observation and *maxime*, that Nature does nothing in vain. It seems, I say, contrary to that great Wisdom of Nature, that these greatly figur'd bodies should have all those curious Figures and contrivances (which many of them are adorn'd and contriv'd with) generated or wrought by a *Plastick virtue*, for no higher end than only to exhibite such a form; which he that shall throughly consider all the circumstances of such kind of Figur'd bodies, will, I think, have great reason to believe, though, I confess, one cannot presently be able to find out what Nature's designs are. It were therefore very desirable, that a good collection of such kind of figur'd stones were collected; and as many particulars, circumstances, and informations collected with them as could be obtained, that from such a History of Observations well rang'd, examin'd and digested, the true original or production of all those kinds of stones might be perfectly and surely known; such as are *Stannaces*, *Lapides Stellares*, *Lapides Judaici* and multitudes of other, whose of mention is made in *Aldrovandus*, *Wormius*, and other Writers of Minerals.

**Observ. XVIII.** *Of the Schematisme or Texture of Cork, and of the Cells and Pores of some other such frothy Bodies.*

I Took a good clear piece of Cork, and with a Pen-knife sharpen'd as keen as a Razor, I cut a piece of it off, and thereby left the surface of it exceeding smooth, then examining it very diligently with a *Microscope*, me thought I could perceive it to appear a little porous; but I could not so plainly distinguish them, as to be sure that they were pores, much less what Figure they were of: But judging from the lightness and yielding quality of the Cork, that certainly the texture could not be so curious,

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curious, but that possibly, if I could use some further diligence, I might find it to be discernable, with a *Microscope*, I with the same sharp Penknife, cut off from the former smooth surface an exceeding thin piece of it, and placing it on a black object Plate, because it was it self a white body, and casting the light on it with a deep *plano-convex Glass*, I could exceeding plainly perceive it to be all perforated and porous, much like a Honey-comb, but that the pores of it were not regular; yet it was not unlike a Honey-comb in these particulars.

First, in that it had a very little solid substance, in comparison of the empty cavity that was contain'd between, as does more manifestly appear by the Figure A and B of the XI Scheme, for the *Interstitia*, or walls (as I may so call them) or partitions of those pores were near as thin in proportion to their pores, as those thin films of Wax in a Honey-comb (which enclose and constitute the *sexangular* cells) are to theirs.

Next, in that these pores, or cells, were not very deep, but consisted of a great many little Boxes, separated out of one continued long pore, by certain *Diaphragms*, as is visible by the Figure B, which represents a sight of those pores split the long-ways.

I no sooner discern'd these (which were indeed the first *microscopical* pores I ever saw, and perhaps, that were ever seen, for I had not met with any Writer or Person, that had made any mention of them before this) but me thought I had with the discovery of them, presently hinted to me the true and intelligible reason of all the *Phænomena* of Cork; As,

First, If I enquir'd why it was so exceeding light a body? my *Microscope* would presently inform me that here was a *reason* evident, that there is found for the lightness of froth, or an empty Honey-comb, Wool, a Sponge, a Pumice-stone, or the like; namely, a very small quantity of a body, extended into exceeding large dimensions.

Next, I could from the same *reason* give an intelligible reason, why Cork is a body so very unapt to suck and drink in Water, and consequently preserves it self, floating on the top of Water, though left on it a long time: and why it is able to stop and hold air or liquors in a Bottle, though through those passages are so exceeding thin and slender. For the interstitia being many of these little partitions of a substance not only apt to suffer but seeming to...

K

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consists of an infinite company of small Boxes or Bladders of Air, which is a substance of a springy nature, and that will suffer a considerable condensation...

FIG. 4.   (PART 1.)

## MICROGRAPHIA.     115

of other Vegetables to do to their bulk. But of these pores I have said more elsewhere.

To proceed then, Cork seems to be by the *texture* and configuration of the pores, a kind of *Fungus* or Mushroom, for the pores lie like so many Rays tending from the center, or equidistant the sides, outwards; so that if you cut off a piece from a board of Cork transversly, to the flat of it, you will, as it were, split the pores, and they will appear just as they are exprest in the Figure B. of the XI. *Scheme*. But if you shave off a very thin piece from this board, parallel to the plain of it, you will cut all the pores transversly, and they will appear almost as they are exprest in the figure A, save only the solid *Interstitia* will not appear so thick as they are there represented.

So that Cork seems to suck its nourishment from the subjacent bark of the Tree immediately, and to be a kind of excrescence, or a substance distinct from the substances of the entire Tree, something *analogus* to the Mushrome, or Moss on other Trees, or to the hairs on animals. And having enquired into the History of Cork, I find it reckoned as an excrescency of the bark of a certain Tree, which is distinct from the two barks that lie within it, which are common also to other trees; That 'tis some time before the Cork that covers the young and tender spruce comes to be distinguishable, That it cracks, flaws, and cleaves into many great chaps, the bark underneath remaining entire; That it may be separated and removed from the Tree, and yet the two under-barks (such as are common to that with other Trees) not at all injur'd, but rather helped and freed from a external injury. Thus *Joysttanus in Penbrokstre*, speaking *de cubers*, says, *Arbor & procera, Lignum (si relaxium, dengus cortex in qua suo fuscus, Cortex in arbore detratto penetra, crescipcum denuo gignit; & torquideo, unde crassamus novus vigetior; Cortex ille adestur crassus, cortex superior denstis crenigis denus legitus crassus, sodus, rumtus, & qui est distrahature detegit, tamque fungositate expellitur, interrumem & leni accedatur in cubus ut orbem denus palis saludatur.* Which Historian well confirm'd, and that very substance, and growing, if well examin'd, would, I am very apt to believe, much confirm this my conjecture about the origination of Cork.

Nor is this kind of Texture peculiar to Cork onely; for upon examination with my *Microscope*, I have found that the pith of an Elder, or almost any other Tree, the inner pulp or pith of the Cany hollow stalks of several other Vegetables: as of Fennel, Carrets, Daucus, Bur-docks, Teasels, Fearn, stalks of divers other Vegetables, &c. have much such a kind of *Schematisme*, as I have lately shewn that of Cork, save onely that here the pores rang'd the long-ways, or that the long ways is the length of the Cane, whereas in Cork they are transverse.

The pith also that fills that part of the stalk of a Feather that is above the Quil, has much such a kind of texture, save onely that which way soever I set it I let this light substance, the pores seem'd to be cut transversly; so that I ghess this pith which fills the feather, not to consist of abundance of long pores separated with *diaphragms*, as Cork does, but to be a kind of

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of solid or hardned froth, or a congeries of very small bubbles consolidated in that form, into a pretty stiff as well as tough concrete, and that each Cavern, Bubble, or Cell, is distinctly separate from any of the rest, without any kind of hole in the encompassing films, so that I could no more blow through a piece of this kind of substance, then I could through a piece of Cork, or the found pith of an Elder.

But though I could not with my *Microscope*, nor with my breath, nor any other way I have yet try'd, discover a passage out of one of those cavities into another, yet I cannot thence conclude, that therefore there are none such, by which the *succus nutritius*, or appropriate juices of Vegetables, may pass through them, for, in several of those Vegetables, whil'st green, I have with my *Microscope*, plainly enough discover'd these Cells or Pores fill'd with juices, and by degrees sweating them out: as I have also observ'd in green Wood all those long *Microscopical* pores which appear in Charcoal perfectly empty of any thing but air.

Now, though I have with great diligence endeavoured to find whether there be any such thing in those *Microscopical* pores of Wood or Pith, as the *Valves* in the heart, veins, and other passages of Animals, that open and give passage to the contain'd fluid juices one way, and shut themselves, and impede the passage of such liquors back again, yet have I not hitherto been able to say any thing positive in it; though, me thinks, it seems very probable, that Nature has in these passages, as well as in those of Animal bodies, very many appropriated Instruments and contrivances, whereby to bring her designs and end to pass, which 'tis not improbable, but that some diligent Observer, if helpt with better *Microscopes*, may in time detect.

And that this may be so, seems with great probability to be argued from the strange *Phænomena* of sensitive Plants, wherein Nature seems to perform several Animal actions with the same *Schematisme* or Organization that is common to all Vegetables, as may appear by some, no less instructive then curious Observations that were made by divers Eminent Members of the *Royal Society* on some of these kind of Plants, whereof an account was delivered in to them by the most Ingenious and Excellent *Hofman*, Doctor *Clark*, which, having that liberty granted me by that most Illustrious Society, I have hereunto adjoyn'd.

*Observations on the Humble and Sensible Plants in Mr. Chiffin's Garden in Saint James's Park, made August the 9th 1661, Present, the Lord Brouncker, Sir Robert Moray, Dr. Wilkins Mr. Evelin, Dr. Henshaw, and Dr. Clark.*

There are four Plants, two of which are little shrub Plants, with a little short stock, about an Inch above the ground, from whence are spread several stichy branches, round, straight, and smooth.

FIG. 4.     (PART 2.)

they gave the Learned World by their justly admired Labours; he was soon taken notice of, and for his Facility in Mechanick Inventions much priz'd by them.

.    .    .    .    .    .    .    .    .    .    .    .    .

"The same Year I contriv'd and made many trials about the Art of flying in the Air, and moving very swift on the Land and Water, of which I shew'd several Designs to Dr. *Wilkins* then *Warden* of *Wadham College,* and at the same time made a Module, which, by the help of Springs and Wings, rais'd and sustain'd itself in the Air; but finding by my own trials, and afterwards by Calculation, that the Muscles of a Mans Body were not sufficient to do anything considerable of that kind, I apply'd my Mind to contrive a way to make artificial Muscles; divers designs whereof I shew'd also at the same time to Dr. *Wilkins,* but was in many of my Trials frustrated of my expectations."[1]

What is mentioned here of his attempts about flying, is confirm'd by several Draughts and Schemes upon Paper, of the Methods that might be attempted for that purpose, and of some contrivances for fastening succedaneous Wings, not unlike those of Bats, to the Arms and Legs of a Man, as likewise of a Contrivance to raise him up by means of Horizontal Vanes plac'd a little aslope to the Wind, which being blown round, turn'd an endless Screw in the Center, which help'd to move the Wings, to be manag'd by the Person by this means rais'd aloft. . . .

.    .    .    .    .    .    .    .    .    .    .    .    .

Soon after the beginning of the ROYAL SOCIETY, *viz.* about *April* 1661. a Debate arose in the Society, occasion'd by a small Tract Printed in 1660. about the cause of the rising of Water in slender Glass Pipes, higher than in larger, and that in a certain proportion to their Bores; this Discourse was wrote and Publish'd by *Hooke;* the Explication of which difficult *Phænomenon* made him the more regarded. The sum of his Reasonings upon this Subject he Publish'd afterward, *Micrography Observ.* the 6th. in which there are several very curious and then new Remarks and Hints; as to the Nature of Fluidity and Gravity, which last is farther prosecuted in his Treatise of Springs, with other excellent Subjects, to which the Inquisitive are referr'd for a more ample satisfaction.

This, together with his former Performances, made him much respected by the *R. Society,* and on the fifth of *November* 1662. "Sir *Robert Moray* propos'd a Person that was willing to be entertain'd as a *Curator* by the *Society,* offering to furnish them every day when they met, with three or four considerable Experiments; which Proposition was unanimously receiv'd, Mr. *Hooke* being nam'd to be the Person; and accordingly the next Day of their meeting on the twelfth of *November* he was unanimously accepted and taken as *Curator,* with the Thanks of the *Society* order'd to Mr. *Boyle* for dispensing with him for their

[1] From Hooke's diary.

use, and order'd that Mr. *Hooke* should come and sit among them, and both bring in every Day three or four of his own Experiments, and take care of such others as should be recommended to him by the *Society*."

<div style="border:1px solid black;">

The Pofthumous

# WORKS

OF

## ROBERT HOOKE, *M.D. S.R.S.*

Geom. Prof. Greſh. *&c.*

Containing his

## Cutlerian Lectures,

AND OTHER

# DISCOURSES,

Read at the MEETINGS of the Illuſtrious

## ROYAL SOCIETY.

IN WHICH

I. The preſent Deficiency of NATURAL PHILOSOPHY is diſcourſed of, with the Methods of rendering it more certain and beneficial.
II. The Nature, Motion and Effects of LIGHT are treated of, particularly that of the *Sun* and *Comets*.
III. An Hypothetical Explication of MEMORY; how the Organs made uſe of by the Mind in its Operation may be Mechanically underſtood.
IV. An Hypotheſis and Explication of the cauſe of GRAVITY, or GRAVITATION, MAGNETISM, *&c.*
V. Diſcourſes of EARTHQUAKES, *their Cauſes* and *Effects*, and Hiſtories of ſeveral; to which are annext, *Phyſical Explications* of ſeveral of the Fables in *Ovid's Metamorphoſis*, very different from other Mythologick Interpreters.
VI. Lectures for improving NAVIGATION and ASTRONOMY, with the Deſcriptions of ſeveral new and uſeful *Inſtruments* and *Contrivances*; the whole full of curious Diſquiſitions and Experiments.

Illuſtrated with SCULPTURES.

To theſe DISCOURSES is prefixt the AUTHOR'S LIFE, giving an Account of his Studies and Employments, with an Enumeration of the many Experiments, Inſtruments, Contrivances and Inventions, by him made and produc'd as Curator of Experiments to the *Royal Society*.

PUBLISH'D

## By *RICHARD WALLER*, R. S. Secr.

*LONDON:*

Printed by SAM. SMITH and BENJ. WALFORD, (Printers to the Royal Society) at the *Princes Arms* in St. *Paul's* Church-yard. 1705.

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*Societati, qua at*
*Opus hoc (E Hredij Peshumis miſit demoga dedit Ric: Waller Reg Societ: Londʒn*
*Basima ſecto May 1715*

FIG. 5.

From this time the *Societies* Journals gave sufficient Testimonials of his Performances, all which would be too many to particularize here, therefore I shall only touch upon some of the chief. . . .

At several Meetings of the *Society* in 1663, and 4. he produc'd his Microscopical Observations, and read the Explications and Discourses made upon them, which were after publish'd in his *Micrographia,* at the beginning of the year 1665.

" Sir *John Cutler* having founded a Lecture, and settl'd an Annual Stipend upon *Robert Hooke,* M.A. of fifty Pounds during Life (entrusting the President, Council and Fellows of the said *Society* to direct and appoint the said Mr. *Hooke* as to the Subject and Number of his Lec-

tures) the *Society* order'd several of their Members to wait upon Sir *John Cutler,* with their Thanks for his particular Favour to a worthy Member, and for that Respect and Confidence he hath hereby exprest towards their whole Body, etc."[2]

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From this time he brought in almost at every Meeting Experiments, Observations, Schemes of new Instruments and Inventions, or something considerable to the advancement of Knowledge, and very frequently read his *Cutlerian* Lectures, of many whereof he publish'd, the most material parts in his Tracts Printed at different times, in Quarto, call'd *Lectures and Collections,* &c. comprizing compendiously in one continu'd Discourse, the chief Matters and Subjects handled in several Lectures.

Thus the generous Ardor with which the Royal Society was inspir'd continued 'till the Year 1665, when, by reason of the great Mortaity then reigning, they were oblig'd to desist and break up their Weekly Meetings till the fourteenth of *March* $166\frac{5}{6}$. . . .

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The dreadful Conflagration of a great part of the City of *London* happening in the beginning of *September* 1666. brought another great hindrance to the *Societies* Proceedings; so that they were oblig'd to remove their usual place of Meeting from *Gresham College* to *Arundel* House in the *Strand,* where, by the favour of the then Duke of *Norfolk,* they prosecuted their former Inquiries, their first Meeting at *Arundel* House being on the ninth of *Jan.* 166 .

On the nineteenth of *Sep.* 1666. he produc'd a Module he had design'd for the Rebuilding of the City, with which the *Society* were very well pleas'd, and Sir *John Laurence* the then Late *Lord Major,* address'd himself to the *Society,* expressing the present *Lord Majors and Aldermens* liking thereof, as also their desire that it might be shewn to his *Majesty,* they preferring it far before the Model drawn up by the City Surveyor.

What this Model was, I cannot so well determine, but I have heard that it was design'd in it to have all the chief Streets as from *Leaden-Hall* corner to *Newgate,* and the like, to lie in an exact strait Line, and all the other cross Streets turning out of them at right Angles, all the Churches, publick Buildings, Market-places, and the like, in proper and convenient places, which, no doubt, would have added much to the Beauty and Symmetry of the whole. How this came not to be accepted of I know not, but it is probable this might contribute not a little to his being taken notice off by the Magistrates of the City, and soon after made Surveyor.

The Rebuilding of the City, according to the Act of Parliament, requiring an able Person to set out the Ground to the several Proprietors,

[2] From the Journal of the Secretary of the Royal Society, November 9, 1664.

Mr. *Hooke* was pitch'd upon, and appointed *City-Surveyor* for that difficult Work, which being very great, took up a large proportion of his Time, to the no small hindrance of his Philosophical Disquisitions.

In this Employment he got the most part of that Estate he died possessed of, as was evident by a large Iron Chest of Money found after his Death, which had been lock'd down with the Key in it, with a date of the Time, by which it appear'd to have been so shut up for above thirty Years: In this was contain'd the greatest part of what he left behind him, which was to the value of many thousands in Gold and Silver. That he might by this place justly acquire considerable Estate, I think cannot be deny'd. . . .

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Mr. *Oldenburgh,* the then Secretary, dying in the time of the Societies Recess, 1677. Mr. *Hooke* was desir'd to take his place, and take the Minutes of what considerable Matters past, which he did on the twenty fifth of *October* 1677. and the same day produc'd his Waterpoise and shew'd the nicety thereof.

From that time he officiated in that Place, as well as his Curatorship, shewing several Experiments and Instruments in order to explain the Gravitation and Alterations in the Air by Vapours, etc. Contriving an Air-poise to shew the different specifick Gravity of the Air by a large thin ball of Glass counter-poised.

. . . . . . . . . . .

From this time he made Microscopical Observations on *Animalcules* in Peper-water, and other Seeds steeped in Water, confirming Monsieur *Leuenhook's* Assertions, and propos'd some Improvements of Microscopes.

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*Apr.* 25. 1678. he shew'd an Experiment farther to explain the action of a Muscle, " which was by a Chain of small Bladders fastened together, so as by blowing into one Pipe, the whole might be successively fill'd, and by that means contracted, supposing the Fibres of the Muscles which seem'd like a Necklace of Pearl in the Microscope, might be fill'd with a very agill Matter, which he thought most likely to be Air, which being included in so thin Skins, was easily wrought upon by Heat, Cold, or the acting Properties of the Liquors that pass between them, and so perform the lengthening and contracting of the Muscles.

Aug. 1678. he read several Discourses, and shew'd Experiments in order to confirm his Theory of Springs and springy Bodies. . . .

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Thus I have mention'd some of his Performances. . . . It must be confessed that the latter part of his Life was nothing near so fruitful of Inventions as the former; tho' it is certain he had a design to repeat the most part of his Experiments, and finish the Accounts, Observations

and Deductions from them, and had an Order for the Societies bearing the Charge thereof, in *June* 1696. when he propos'd likewise to perfect the Description of all the Instruments he had at any time contriv'd; but by reason of his increasing Weakness and a general Decay, he was absolutely unable to perform it, had he desir'd it never so much.

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Thus he liv'd a dying Life for a considerable time, being more than a Year very infirm, and such as might be call'd Bed-rid for the greatest part, tho' indeed he seldom all the time went to Bed. . . . being emaciated to the utmost, his Strength wholly worn out, he dy'd on the third of *March* 170$\frac{2}{3}$. being 67 Years, 7 Months, and 13 Days Old.

His Corps was decently and handsomely interr'd in the Church of St. *Hellen* in *London*, all the Members of the Royal Society then in Town attending his Body to the Grave, paying the Respect due to his extraordinary Merit.

As to his Person he was but despicable, being very crooked, tho' I have heard from himself, and others, that he was strait till about 16 Years of Age when he first grew awry, by frequent practicing with a Turn-Lath, and the like incurvating Exercises, being but of a thin weak habit of Body, which increas'd as he grew older, so as to be very remarkable at last: This made him but low of Stature. . . . He went stooping and very fast (till his weakness a few Years before his Death hindred him) having but a light Body to carry, and a great deal of Spirits and Activity, especially in his Youth.

He was of an active, restless, indefatigable Genius even almost to the last, and always slept little to his Death, seldom going to Sleep till two three, or four a Clock in the Morning, and seldomer to Bed, often continuing his Studies all Night, and taking a short Nap in the Day. His Temper was Melancholy, Mistrustful and Jealous, which more increas'd upon him with his Years. He was in the beginning of his being made known to the Learned, very communicative of his Philosophical Discoveries and Inventions, till some Accidents made him to a Crime close and reserv'd. He laid the cause upon some Persons, challenging his Discoveries for their own, taking occasion from his Hints to perfect what he had not; which made him say he would suggest nothing till he had time to perfect it himself, which has been the Reason that many things are lost, which he affirm'd he knew. He had a piercing Judgment into the Dispositions of others, and would sometimes give shrewd Guesses and smart Characters.

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It must be confess'd that very many of his Inventions were never brought to the perfection they were capable of, nor put in practice till some other Person either Foreigner or of our own Nation cultivated the Invention, which, when Hooke found, it put him upon the finishing that which otherwise possibly might have lain 'till this time in its first

Defects: Whether this mistake arose from the multiplicity of his Business which did not allow him a sufficient time, or from the fertility of his Invention which hurry'd him on, in the quest of new Entertainments, neglecting the former Discoveries when he was once satisfied of the feazableness and certainty of them, tho' there wanted some small matter to render their use more practicable and general, I know not. . . .

Whatever the answer may be, Hooke's first and best known work, the Micrographia, at once epitomizes the versatility of his genius as well as his apparent inability to see one problem through to a finish.   To quote from a review of the work in the *Philosophical Transactions,* No. 2, Monday, April 3, 1665:

The Ingenious and knowing Author of this *Treatise,* Mr. *Robert Hook,* considering with himself, of what importance a faithful *History of Nature* is to the establishing of a solid Systeme of *Natural Philosophy,* and what advantage *Experimental* and *Mechanical* knowledge hath over the Philosophy of *discourse* and *disputation,* and making it, upon that account, his constant business to bring into that vast Treasury what portion he can, hath lately published a Specimen of his abilities in this kind of study, which certainly is very welcome to the Learned and Inquisitive world, both for the *New discoveries* in *Nature,* and the *New Inventions* of *Art.*

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To this end, he hath made a very curious *Survey* of all kinds of bodies, beginning with the *Point of a Needle,* and proceeding to the *Microscopical* view of the *Edges of Rasors, Fine Lawn, Tabby, Watered Silks, Glass-canes, Glass-drops, Fiery Sparks, Fantastical Colours, Metaline Colours, the Figures of Sand, Gravel in Urine, Diamonds in Flints, Frozen Figures, the Kettering Stone, Charcoal, Wood and other Bodies petrified, the Pores of Cork, and of other substances, Vegetables growing on blighted Leaves, Blew mould and Mushroms, Sponges, and other Fibrous Bodies, Sea-weed, the Surfaces of some Leaves, the stinging points of a Nettle, Cowage, the Beard of a wild Oate, the seed of the Corn-violet,* as also of *Tyme, Poppy and Purslane.*   He continues to describe *Hair, the scales of a Soal, the sting of a Bee, Feathers* in general, and in particular those of *Peacocks; the feet of Flies; & other Insects; the Wings and Head of a Fly; the Teeth of a Snail; the Eggs of Silk-worms; the Blue Fly; a water Insect; the Tufted Gnat; a White Moth; the Shepherds-spider; the Hunting Spider, the Ant; the wandring Mite; the Crab-like insect, the Book-worm, the Flea, the Louse, Mites, Vine-mites.*   He concludeth with taking occasion to discourse of two or three very considerable subjects, viz. *The inflexion of the Rays of Lights in the Air; the Fixt starrs; the Moon.*

In representing these particulars to the Readers view, the Author hath not only given proof of his singular skil in delineating all sorts of Bodies (he having drawn all the *Schemes* of these 60 *Microscopical* objects with his own hand) & of his extraordinary care of having them so curiously engraven by the Masters of that Art; but he hath also suggested in the several reflexions, made upon these Objects, such conjecturs, as are likely to excite and quicken the Philosophicall heads to very noble contemplations.   Here are found inquiries concerning the *Propagation of Light* through differing mediums; concerning *Gravity;* concerning the *Roundness* of Fruits, stones, and divers artificial bodies; concerning *Springiness* and *Tenacity;* concerning the *Original* of *Fountains;* concerning the *dissolution of Bodies into Liquors;* concerning *Filtration,* and the ascent of Juices in Vegetables, and the use of their *Pores.*   Here an attempt is made of solving the strange *Phænomena of Glass-drops;* experiments are alleged to prove the *Expansion* of *Glass* by heat, and the *Contraction* of *heated-Glass* upon cooling; *Des Cartes* his *Hypothesis of colours* is examined: the *cause of Colours,* most likely to the Author, is explained: Reasons are produced, that *Reflection* is not necessary to produce *colours,* nor a *double refraction:* some considerable *Hypotheses* are *offered,* for the explication of Light by Motion; for the producing of all colors by Refraction; for reducing all sorts of colors to two only, *Yellow* and *Blew;* for making the *Air,* a dissolvent of all *Combustible Bodies:* and for the explicating of all the regular figures of *Salt,* where he alleges many notable instances of the *Mathematicks* of *Nature,* as having even in those things which we account vile, rude and coorse, shewed abundance of curiosity and excellent *Geometry* and *Mechanism.*   And here he opens a large field for inquiries, and proposeth Models for prosecuting them. . . .

He goes on to offer his thoughts about the Pores of bodies, and a *kind* of *Valves* in wood; about spontaneous generation arising from the Putrefaction of bodies; about the nature of the Vegetation of mold, mushromes, moss, spunges; to the last of which he scarce finds any Body like it in texture.   He adds, from the naturall contrivance, that is found in the leaf of a Nettle, how the stinging pain is created, and thence takes occasion to discourse of the poysoning of Darts.   He subjoyns a curious description of the shape, *Mechanism* and use of the *sting* of a *Bee;* and shews the admirable Providence of Nature in the contrivance and fabrick of *Feathers* for Flying.   He delivers those particulars about the Figure, parts and use of the head, feet, and wings of a Fly, that are not common.   He observes the various wayes of the generations of Insects, and discourses handsomely of the means, by which they seem to act so prudently.   He taketh notice of the *Mechanical* reason of the *Spider's* Fabrick, and maketh pretty Observations on the hunting Spider, and other Spiders and their Webs.   And what he notes of a Flea, Louse, Mites and Vinegar-worms, cannot but exceedingly please the curious Reader.

Having dispatched these Matters, the Author offers his Thoughts for the explicating of many *Phænomena* of the Air, from the *Inflexion,* or from a *Multiplicate Refraction* of the rays of Light within the Body of the *Atmosphere,* and not from a *Refraction* caused by any terminating *superficies* of the Air above, nor from any such exactly defin'd *superficies* within the body of the *Atmosphere.* . . . .

He concludeth with two *Celestial Observations;* whereof the *one* imports, what multitudes of Stars are discoverable by the Telescope, and the variety of their magnitudes . . . the other affords a description of a *Vale* in the *Moon,* compared with that of *Hevelius* and *Ricciolo;* where the Reader will find several curious and pleasant Annotations . . . about the variations in the *Moon,* and its *gravitating* principle, together with the use, that may be made of this Instance of a gravity in the *Moon.*

As to the *Inventions of Art,* described in this Book, the curious Reader will there find these following:

1. A *Baroscope,* or an Instrument to shew all the Minute Variations in the *Pressure of the Air;* by which he affirms, that he finds, that before and during the time of rainy weather, the Pressure of the Air is less. . . .

2. A *Hygroscope,* or an Instrument, whereby the *Watery steams,* volatile in the Air, are discerned, which the Nose it self is not able to find. Which is by him full described in the Observations touching the *Beard of a wild Oate,* by the means whereof this Instrument is contrived.

3. An Instrument for *graduating Thermometers,* to make them *Standards* of *Heat* and *Cold.*

4. A *New Engin* for *Grinding Optik Glasses,* by means of which he hopes, that any Spherical Glasses, of what length soever, may be speedily made. . . .

5. A *New Instrument,* by which the *Refraction* of all kinds of Liquors may be exactly measured, thereby to give the Curious an opportunity of making Trials of that kind, to establish the *Laws of Refraction.* . . .

Lastly, this Author despairs not that there may be found many Mechanical Inventions, to improve our Senses of *Hearing, Smelling, Tasting, Touching,* as well as we have improved that of *Seeing* by *Optick Glasses.*

Thus the "Micrographia" is obviously something more than "Some Physiological Descriptions of Minute Bodies made by Magnifying Glasses"—it is a demonstration of the advantages to be gained by the use of artificial devices of precision in studying nature. The book is replete with singular anticipations of later discoveries and inventions by other workers and "it will hardly be deny'd that there are more excellent Philo-

sophical Discoveries and Hints, than in most extant of its bulk.'' It contains the first study of the '' fantastical colours'' of thin plates with a partial explanation by interference; a theory of light as a ''very short vibrating motion'' transverse to straight lines of propagation through a ''homogenous medium'' (p. 56). Heat is stated to be ''a property of a body arising from the motion or agitation of its parts'' (p. 37); Fluidity is ''but an effect of a very strong and quick shaking motion, whereby the parts are, as it were, loosened from each other, and consequently leave an interjacent space or vacuity'' (p. 41); while ideas in regard to combustion are clearly outlined (p. 103) which foreshadow those reached by Mayow.

But the biologist's interest in the ''Micrographia'' is chiefly in Hooke's application of his improved compound microscope (Fig. 2) to the study of animals and plants. At this time Malpighi, Grew, Leeuwenhoek and Swammerdam were engaged in studies, with simple lenses or compound microscopes, on the secrets of the finer structure of organisms which were to give them higher rank in biological history than Hooke's desultory work in this field. Hooke, as has been said, was interested primarily in demonstrating the usefulness of his microscope and his belief that in inventions for the ''improvement of the senses'' lay the key to a more profound understanding of nature. This he accomplished and therefore, entirely aside from the other remarkable qualities of the ''Micrographia,'' the book holds a unique place in the history of biology. It paved the way, as it were, for the more special, profound and methodical studies of the contemporary founders of the morphology of organisms by creating a considerable interest in microscopy, and in addition proved to be for over a century the standard source from which writers on the microscope gleaned much information and many figures.[3]

[3] E. g., L. Joblot, 2d Ed., 1754; H. Baker, 1742; M. F. Ledermüller, 1760–1763; etc. In 1745 Baker reprinted and explained the plates of the Micrographia.

Among the large variety of observations made by Hooke, which are cited in Oldenburg's review just quoted in extenso, one in particular claims the attention of the biologist. This is "Observation XVIII. Of the Schematisme or Texture of Cork, and of the Cells and Pores of some other such frothy Bodies." Here are clearly described for the first time the "little boxes or cells" of organic structure, and his use of the word "cell" is responsible for its application to the protoplasmic units of modern biology. This observation, together with the plate, is presented in facsimile in Figs. 3 and 4. In Hooke's treatise on " The method of Improving Natural Philosophy," included in the volume of his posthumous works (p. 28), this observation on cells is selected by Hooke to illustrate his method of scientific inquiry.

Again, "Observation XXV. Of the stinging points and juice of Nettles, and some other Venomous Plants" is accompanied by a figure of the lower side of a nettle leaf in which the outlines of the epidermal cells are well delineated and, as Miall remarks, "there is something very like a nucleus in one of them, but this may be accidental." However, Hooke did not recognize any relationship between the structures he observed in the nettle and in the cork.

As an appendix to his observations on cork, the author relates some experiments on Mimosa in which he attributes the "motion of this Plant upon touching . . . to a constant *intercourse* betwixt every part of this Plant and its root, either by a *circulation* of its liquor, or a constant pressing of the subtiler parts of it to every extremity of the Plant"—a partial anticipation of the modern idea of turgescence (cf. Figs. 3 and 4). The "Observation on Petrify'd wood and other Petrify'd bodies" is interesting because the author takes quite a modern point of view in regard to fossils (cf. Fig 4, Part I).

And so we might continue—but as the reviewer remarks in the *Journal des Scavans,* December, 1666: "This Book contains more than can be taken notice of in an

Extract,'' and we conclude the survey of this man of the past still using the words of the past:

All his Errors and Blemishes, were more than made amends for, by the Greatness and Extent of his natural and acquired Parts, and more than common, if not wonderful Sagacity, in diving into the most hidden Secrets of Nature, and in contriving proper Methods of forcing her to confess the Truth, by driving and pursuing the *Proteus* thro' all her Changes, to her last and utmost Recesses; so that what *Ovid* said of *Pythagoras* may not unfittly be apply'd to him.

> *Mente Deos adiit, et quae Natura negavit*
> *Visibus humanis, oculis ea Pectoris hausit.*

There needs no other Proof for this than the great number of Experiments he made, with the Contrivances for them, amounting to some hundreds; his new and useful Instruments and Inventions, which were numerous, his admirable Facility and Clearness, in explaining the Phænomena of Nature, and demonstrating his Assertions; his happy Talent in adapting Theories to the Phænomena observ'd, and contriving easy and plain, not pompous and amusing Experiments to back and prove those Theories; proceeding from Observations to Theories, and from Theories to farther trials, which he often asserted to be the most proper method to succeed in the interpretation of Nature. For these, his happy Qualifications, he was much respected by the most learned Philosophers both at home and abroad: And as with all his Failures, he may be reckon'd among the great Men of the last Age, so had he been free from them, possibly, he might have stood in the Front. But *humanum est errare*.[4]

[4] Waller, *op. cit.*

# SHORTER ARTICLES AND DISCUSSION.

## SIAMESE, AN ALBINISTIC COLOR VARIATION IN CATS

COMPARATIVE studies of color inheritance in mammals have shown that pigment production throughout the group is due to similar processes and to genes probably homologous. These studies have shown, for example, that the pink-eyed albino condition seen in white rabbits, white rats, white mice and white guinea-pigs behaves in all cases as a simple recessive in crosses. It is probably due to variation in the same (*i. e.*, in an homologous) genetic locus in all these rodents. In its usual form albinism consists in a complete absence of pigmentation from the ectoderm of the embryo and from all derivatives of that germ-layer in the adult animal. This includes, not only the hair, but also the retina and iris of the eye. Such is the condition seen in the white mouse, the white rat, and the "Polish" or "Russian" rabbit. But this same locus may apparently undergo a different change which, while it behaves as the perfect allelomorph of the pure white albino variation, differs from it in that it allows a certain amount of pigment to be produced, more particularly in the retina of the eye and in the hair at the extremities of the body (nose, ears, tail and feet). At times a small amount of pigment is formed elsewhere throughout the coat. This condition is best known in the "Himalayan" rabbit. Clear white albinism of the Polish rabbit is an allelomorph of Himalayan albinism. In the guinea-pig only the Himalyan type of albinism is known; in rats and mice, only the Polish type is known.

In the guinea-pig, Wright has demonstrated the existence of two other albino allelomorphs, which apparently are distinct mutations of the same genetic locus. These are found in the red-eyed and in the dilute varieties described by him. Among rats Whiting and King have demonstrated the existence of a variety comparable with the dilute varieties of guinea-pigs and which they call "ruby-eyed." It behaves as an allelomorph of ordinary albinism in crosses.

White spotting of colored animals, sometimes called "partial albinism," is an entirely different variation, due to variation in a different locus. True albinism and spotting may by suitable crosses be made to coexist in the same individual. In this way

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I have frequently produced *spotted* Himalayan rabbits, which would show particular types of white spotting, as Dutch or English, on the feebly pigmented Himalayan background (as has also Punnett), and Wright has produced whole series of varieties of spotted red-eyed and spotted dilute guinea-pigs.

Among certain rodents pink-eyed varieties occur which are due to variation in a genetic locus wholly distinct from that which is responsible for albinism. Such are the well-known pink-eyed varieties of mice having colored coats. Here the retina and the fur alike have a greatly reduced amount of black and brown pigmentation as compared with normal individuals, though yellow is unaffected. Pink-eyed rats and pink-eyed guinea-pigs are similar in appearance and in genetic behavior to pink-eyed mice. When crossed with the albino variety of the same species, they produce fully colored offspring as regards both eye and coat. The gene for pink-eye is thus seen to be complementary to the gene for albinism, with which it is known to be "linked" in rats and mice. Whether the two are also "linked" in guinea-pigs has not yet been ascertained.

Among mammals other than rodents albino and pink-eyed varieties are not certainly known to occur, though white-spotted and black-eyed white varieties are common. It is thus an open question whether the same genetic loci are found among them as among rodents. Bateson has pointed out similarities between a color variety of cat, the so-called Siamese, and the Himalayan variety of rabbit. Both are born white or nearly white and later become more heavily pigmented. I may add (2) that both are inherited as recessives and (3) that in both varieties yellow pigment is largely or wholly suppressed, which is characteristic of the albino variation, but not of the pink-eye variation of rodents.

Wright has suggested that blondism among human beings (which when extreme in character is commonly known as albinism) is similar in nature to the albinism of rodents, being a graded series of allelomorphs similar to the series which he has described in the guinea-pig.

It thus appears probable that the same genetic locus, which occurs in rodents and which has been called the "color factor," occurs also in other mammals, including man.

The case of the Siamese cat has seemed to me for some years deserving of more careful study. Lacking opportunity for such study myself, I sent out an inquiry several years ago through

the pet-stock journals for information about Siamese cat crosses A single reply has just come to hand, but from an authoritative source. A doctor, who prefers to remain anonymous, resident in an extensive institution in England and a fancier of Siamese cats, has employed his leisure, and the unusual opportunities afforded by his position, in studying the genetic behavior of Siamese cats in crosses with other varieties. He regards as characteristics of the Siamese breed a peculiar quality of voice and "cross-eyes," which characters often are seen in first generation crosses and so would seem to be inclined to dominance. But the distinctive Siamese color, he states, is never seen in $F_1$ individuals, "although quite a number show a midway color. At a glance you would say they were black, but on more careful examination you see they are near the color of the Siamese ears, seal brown. Most first crosses in my experience are black or seal, but some tortoise shell, or tortoise shell and white, or black and white." These statements indicate the usual behavior of yellow and of white-spotting in cat crosses. (See Whiting, 1918.) The Siamese color is evidently an independent character incompletely recessive in $F_1$. The doctor continues his account with a brief statement concerning a back cross of $F_1$ with pure Siamese. "I have a first cross female, black seal color, marked cross eyes, Siamese voice. She has been twice mated with a pure Siamese male. In her first litter she had two pure Siamese, perfect Siamese color. Unfortunately both died of distemper when about three months old. Her second mating resulted in one pure Siamese which is still alive. It is about five months old and is perfect in all Siamese points and fit to win [at shows]." Presumably the same sort of back-cross matings as these would produce also kittens similar to the $F_1$ mother in color character, although no mention is made of them in these notes. The information given suffices to show the segregation of Siamese color as a recessive character in generations later than $F_1$. The doctor confirms the observation of others as to the deficient pigmentation of the eye, a point of resemblance with allelomorphs of true albinism, as seen, for example, in red-eyed guinea-pigs (Castle and Wright), and in ruby-eyed rats (Whiting). He says: "The reflex which the Siamese cat shows in the dark is worth notice. It looks blood red and must be due to absence of pigment in the retina." A further point of resemblance with albinism is its distinctness from dilution as seen in "blue" varieties. The doctor speaks of having produced

four Siamese which are "blue-pointed," presumably as a result of crosses with maltese, which are blue pigmented. An exactly similar combination I have recently secured in crossing rabbits, obtaining Himalayans with blue points in $F_2$ from a cross between ordinary black-pointed Himalayans and a self-colored rabbit which carried blue as a recessive character.

To summarize, we have the following indications that Siamese coloration in cats is a form of true albinism similar to that of the Himalayan rabbit, and still more closely resembling the ruby-eyed rat and the red-eyed guinea-pig, all of which species possess also more typical forms of albinism, but which are allelomorphs of those mentioned.

(1) Siamese coloration in cats is attended by a deficiency in amount of pigmentation in both coat and eye. (2) Yellow pigment is more affected than black or brown pigment. (3) The pigmentation is less at birth than at a later period. (4) The character is recessive in heredity. (5) It is distinct from "blue" dilution since it can be combined with it by suitable crosses.

Siamese in cats as far as reported occurs only in a non-agouti form, as does Himalayan in rabbits bred for exhibition. But by a cross with agouti rabbits, Himalayan rabbits are obtained in $F_2$ which have agouti points. As this makes the contrast of points with body less strong, fanciers' standards do not recognize the combination. Nevertheless the experiment shows agouti to be due to a genetic factor distinct from Himalayan. If Siamese in cats is also distinct from agouti, it may be expected that a cross of Siamese with tabby would produce Siamese tabbies in $F_2$, though the combination would probably not be pleasing to the fancier.

<div align="right">W. E. CASTLE.</div>

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## THE MORPHOLOGICAL BASIS OF SOME EXPERIMENTAL WORK WITH MAIZE

OF all the plants that have been made to contribute to our knowledge of the principles of evolution and heredity in the last twenty years, probably none holds a more conspicuous place than Indian corn. The technique of its manipulation is comparatively simple, and it exhibits an extreme variability, which is almost unique in extending to the endosperm; the behavior of a large number of its characteristics has been found amenable to a Mendelian interpretation and has aided materially in establishing present-day views of heredity. Indeed, maize shares with *Pisum* the distinction of having been the means of the establishing of Mendelism itself, for it was in connection with their work on maize that Correns and De Vries discovered Mendel's paper. Since then its genetic behavior has been studied in detail by a number of investigators, and there is probably no other one plant that furnishes such a wealth of material illustrative of the principles of heredity.

The writer has in recent years had the opportunity of examining in more or less detail this same plant from the morphological point of view, and it has been found that we are far more familiar with the Mendelian behavior of some of its characteristics than we are with the characteristics themselves. This has led to some results illustrative of the need of very close coordination between genetics and morphology.

In one of the numerous experiments made by East and Hayes, an attempt was made to interpret the Mendelian behavior of the irregularity of the rows of grains on the ear of corn. The ratios produced in the breeding experiments[1] were not very significant, and, after suggesting the possibility of "monohybridism with reversed dominance," "fluctuating dominance," etc., they finally conclude that "it seems probable that a more complex set of conditions exists."

If, as is suggested, this irregularity is similar to that in Country Gentleman sweet corn, it was probably another set of conditions that caused the trouble. As the writer has since pointed out,[2] the irregularity in the rows of this variety is the more or less complete expression of a very definite and comparatively simple state of affairs. Each female spikelet of ordinary maize

[1] "Inheritance in Maize," Bull. Conn. Agr. Expt. Sta., 167, 1911, p. 132.

[2] "The Morphology of the Flowers of *Zea Mays*," *Bull. Torrey Club*, 43: 127–144, 1916.

produces one grain; but in Country Gentleman sweet corn, a second flower, ordinarily aborted, becomes functional, and the spikelet produces two grains. Since there is little or no compensation for this in the length of the cob, and insufficient difference in the size and shape of the grain, the ear is producing a larger volume of embryo and endosperm than is ordinarily produced in the same space. As a result of this crowded condition, the straight rows are more or less obliterated for a more economical arrangement. At times, however, a set of conditions, presumably environmental, may limit the size of the grain or increase the length of the cob sufficiently that the rows are almost straight, although each spikelet is still producing two grains. The genetic experiment, then, was probably dealing with an indefinite expression of a definite characteristic. If the heredity of the two-flowered condition of the spikelet had been tested, a more direct explanation would probably have been afforded.

Again (p. 134), these same authorities explain the occurrence of hermaphrodite flowers upon the basis that "the immature sex organs, so-called, of maize seem endowed with the power of becoming either stamens or carpels." In so far as actual genetic results are concerned, this is, in most cases, at least, a sound working basis, but it is far from exact morphologically. There is no organ in the young maize flower that has the possibility of becoming in some cases a stamen and in others a pistil. The young flower has the ability to become either staminate or pistillate because it contains primordia of both stamens and a pistil, one or the other of which usually does not develop to maturity.[3]

Blaringhem's extensive experiments,[4] in which he attempts to initiate mutation by means of injuries to the plant, fail to take into full account certain very significant facts of morphology. It is probably for this reason that he believes that the acquisition of hermaphrodite flowers in the maize plant is a *progressive* step. On the contrary, every indication points to the fact that the rudimentary stamens and pistils that have been found in the flowers of maize are the vestiges of organs that have been, and not the phylogenetic forerunners of organs that are to be. Moreover, normal behavior shows that in mutilating the plants he had merely promoted the production of suckers, which normally tend to have bisexual inflorescences. Blaringhem's method is ingenious and would, no doubt, give good results in a study of physiology of monoecism; but, the normal plant being under-

[3] *Ibid.*, pp. 129–134.

[4] Blaringhem, L., "Mutation et traumatismes," Paris, 1908.

stood, and full allowance being made for the recognized effects of inbreeding, it is not believed that there is any clear evidence that he produced a single *new* hereditary characteristic in maize.

But not all of the assumptions of fundamentals upon which geneticists have based their work on maize have been so unhappily chosen as those cited.   Most of the work that has been done on the heredity of endosperm characters depends upon the so-called "double fecundation" and upon the degeneracy of three of the four potential megaspores.   The former of these facts was observed by Guignard[5] in 1901, but he did not figure it; the latter has been deduced by analogy.   Circumstantial evidence was good in both cases, but evidence of this kind is not always dependable.   No one would risk much in a financial way on chances like these, but some geneticists have risked years of work.   In a recent paper[6] the writer has verified the facts assumed in this work.

The peculiar behavior of reciprocal crosses between varieties of corn differing in the physical nature of the starchy endosperm, has been explained[7] by the assumption that the two hereditary factors presumably carried by the two polar nuclei be dominant to the one factor carried by the sperm entering into the constitution of the primary endosperm nucleus.   This idea is in accord with the multiple factor hypothesis, and the phenomenon is one of the few *direct* evidences that we have as to the behavior of a double application of a factor as opposed to a single application of its allelomorph.   But so little is known of the morphology and the chemistry of these two kinds of starch and their relation to the surrounding tissues that it is not at all improbable that the explanation advanced may be modified by the results of further investigation.

An interesting light is thrown upon the the multiple factor theory by certain other morphological peculiarities of the grain of corn.   The essential idea of the multiple factor hypothesis, in a simple form, is that a single visible effect may be due to two or more factors, only one of which is necessary to produce the same effect, at least in a limited degree.   Little is known of the relative natures of the two or more factors that compose the multiple unit in the cases that have been investigated; they may be

[5] Guignard, L., "La double fécondation dans le Maïs." *Jour. de Bot.*, 15: 37–50, 1901.

[6] "Gametogenesis and Fecundation as the Basis of Xenia and Heredity in the Endosperm of *Zea Mays*," *Bull. Torrey Club*, 46: 73–90, 1919.

[7] Hayes, H. K., and East, E. M., "Further Experiments on Inheritance in Maize," *Bull. Conn. Agr. Expt. Sta.*, 188, pp. 12–13, 1915.

alike, or they may be very different from each other.  A grain of corn homozygous for yellow starch and red aleurone is different in color from one having only one of these characteristics. But to a person with defective vision, or when viewed in a light of proper color, these two colors and a combination of the two may appear to be merely different shades of one color.  By breeding this stock with a homozygous white, carrying no conflicting factors, we should get what would be to this same defective vision a perfect illustration of the behavior of multiple factors.  But it is in reality a case of dihybridism in which we have failed to distinguish between the two sets of allelomorphs.  And who can doubt that relatively as great a lack of discrimination may characterize our chemical, physical, or morphological vision in observing some of the classical illustrations to which the multiple factor hypothesis is applicable?

Other examples could be selected from the work that has been done on maize, and doubtless many are available from the investigations made with other plants and with animals, but these will suffice for illustration.  Many of the organisms most useful for establishing and testing principles of heredity have an external appearance that may be very deceptive as an indicator of their true structure, and the true structure alone is the key to the deeper significance of their genetic behavior.

<div align="right">Paul Weatherwax</div>

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## ON HETEROPHYLLY IN WATER PLANTS

THE occurrence of two or more different types of leaf upon one individual, which is so frequently characteristic of water plants, has long attracted the interest of botanists.  The most usual case is that in which the submerged leaves are finely divided while the floating or aerial leaves are relatively simple.  Lyte's Herbal (1578) contains a vivid description of this type of heterophylly in the water buttercup.  Since this description is also noteworthy for its insistence on the influence of external conditions, it may be cited here.

Amongst the fleeting [floating] herbes, there is also a certayne herbe whiche some call water Lyverworte, at the rootes whereof hang very many hearie strings like rootes, the which doth oftentimes change his uppermost leaves according to the places where as it groweth.  That whiche groweth within the water, carrieth, upon slender stalkes, his leaves very small cut, much like the leaves of the common Cammomill,

but before they be under the water, and growing above about the toppe
of the stalkes, it beareth small rounde leaves, somewhat dented, or un-
evenly cut about.  That kind whiche groweth out of the water in the
borders of diches, hath none other but the small jagged leaves.  That
whiche groweth adjoyning to the water, and is sometimes drenched or
overwhelmed with water, hath also at the top of the stalkes, small
rounde leaves, but much more dented than the round leaves of that
whiche groweth alwayes in the water.

Among certain Nymphæaceæ we find a different type of hetero-
phylly in which the submerged leaves are large, thin and translu-
cent, somewhat resembling the seaweed *Ulva*.  These leaves are
particularly well shown in the yellow water-lily.

To enumerate all the varieties of submerged leaf met with
among angiosperms would be too long a task to undertake in the
present paper.  It must suffice to say that they are either highly
divided, ribbon-like, or else thinner and broader than the cor-
responding air leaves.  They are characterized anatomically by
the lack of stomates and by the presence of chlorophyll in the
epidermis.  They are thus well suited for the absorption of car-
bon dioxide in the dissolved form in which it presents itself to
water plants.

In considering the significance of heterophylly, it is a matter of
importance to remember that the occurrence of different leaf-
forms in a single individual is not confined to aquatics but occurs
also in terrestrial plants.  Nehemiah Grew, as long ago as 1682,
pointed out that in many cases one plant bears leaves

of Two Kinds or Two distinct *Figures;* as the *Bitter-sweet,* the common
*Little Bell, Valerian, Lady-Smocks,* and others.  For the *Under leaves*
of *Bitter-Sweet,* are Entire; the Upper, with two *Lobes:* the Under
*Leaves* of the *Little Bell,* like those of *Pancy;* the Upper, like those of
*Carnation,* or of *Sweet William.*

We find parallels to the heterophylly of hydrophytes, not only
among terrestrial flowering plants, but also in the case of the dis-
tinct "youth forms" of conifers, and even—more remotely— in
the *"Chantransia"* stage of such algæ as *Batrachospermum.*
Heterophylly is indeed so widespread that no interpretation can
be valid unless the condition be treated broadly as a very general
attribute of plant life, rather than as a rare and exceptional phe-
nomenon, for which special and individual explanations will
suffice.

To the earlier writers, such as Lamarck, the problem of hetero-
phylly presented no difficulties.  They regarded the submerged
or aerial type of leaf as representing a direct response, on the

part of the plant, to the medium. The work of the last thirty years has, however, rendered this simple conception untenable; the theory that now holds the field accords a much less prominent place to adaptation. The first observation that shook the foundations of the idea that leaf form necessarily depended directly on the milieu, was that of Costantin, who showed that, in the case of *Sagittaria*, the aquatic and aerial leaves were already differentiated from one another in the submerged bud; he noticed auricles on a leaf which was only 2 to 3 mm. long. In *Ranunculus heterophyllus*, also, the leaves destined to be aerial are differentiated in the bud.

A large amount of experimental work has been published by various authors on the effect of conditions upon the leaf forms of heterophyllous plants, and, although some of the results are confused and conflicting, a study of the literature seems to justify one general conclusion—namely, that, in many cases, the submerged type of leaf is, in reality, the juvenile form, but can be produced later in the life history in consequence of poor conditions of nutrition; the air leaf, on the other hand, is the product of the plant in full vigor and maturity. This conclusion, which is primarily due to Goebel and his pupils, is substantiated not only by experiments but by observations in the field.

In many heterophyllous plants, the first leaves produced by a seedling, whether it develops on land or in water, conform, more or less, to the submerged type. This is the case for instance, in the Alismaceæ. In *Alisma plantago*, the water plantain, and *Sagittaria sagittifolia*, the arrowhead, the first leaves produced by the seedling (or the germinating tuber) are ribbonlike, even when the young plant is terrestrial. The formation of this type of leaf can be induced again, even in maturity, by conditions which cause a general weakening of the plant. Costantin thirty years ago, recorded that, when the leaves of *Alisma plantago* were cut off in the process of clearing out a water course, or in a laboratory experiment, the next leaves produced were ribbon-like, thus representing a regression to the submerged form. More recently, another worker, Wächter, tried the experiment of cutting off the roots of healthy, terrestrial plants of *Sagittaria natans* bearing leaves with differentiated laminæ. It was necessary to cut the roots away every week, as they grew again so rapidly. The result of this treatment was that the plants were found to revert to the juvenile stage, the new leaves being band shaped. When the experimenter ceased to interfere with the roots, the plants again formed leaves with laminæ. Other plants,

with uninjured roots, grown as water-cultures in distilled water, also produced the juvenile leaf form, while those grown in a complete culture solution developed their laminæ normally.

The same observer recorded a case in which a plant of *Hydrocleis nymphoides* Buchenau (Butomaceæ), which had been bearing the mature form of leaf, was observed to revert to the ribbon form. On examination it was found that most of the roots had died off. When a fresh crop of roots was produced, the mature type of leaf occurred again.

Another writer, Montesantos, showed by a series of experiments upon *Limnod im Boscii* (Hydrocharitaceæ) that, in this case also, the heterophylly is not a direct adaptation to land or water life, but that the floating leaves are "Hemmungsbildungen" due to poor nutrition. In the water soldier, *Stratiotes aloides*, also, he showed that the stomateless leaves were primary, but that their production could be induced at later stages by unfavorable conditions.

An experiment tried by Goebel on *Sagittaria sagittifolia* indicated that absence of light in this case inhibits the formation of leaves of the aerial type. An observation of Glück's on *Alisma graminifolium* Ehrh., also points to the same conclusion. But it seems probable that the effect produced in these cases was not due directly to the darkness, but to the state of inadequate nutrition brought about by the lack of light for carbon assimilation.

Among the potamogetons, again, experimental work by Esenbeck has shown that reversion to juvenile leaves can be obtained under conditions of poor nutrition. For example, when a land plant of *P. fluitans*, which had been transferred to deep distilled water, had its adventitious roots repeatedly amputated, regression was obtained to the floating type of leaf and then the submerged type. A similar reversion to thin narrow leaves was brought about in the case of *P. natans* by growing the upper internodes of a shoot as a cutting.

Water lily leaves respond to experimental treatment in just the same way as the monocotyledons already mentioned. In the case of two species of *Castalia*, it has been found possible to induce the mature plants to form submerged leaves, either by removing the floating leaves or by cutting off the roots. This confirms an earlier suggestion, made by an Italian writer, Arcangeli, that the development of the submerged leaves of *Nymphæa lutea* was due to "un indebolimento o diminuzione di energia vitale." This suggestion has received independent, experimental confir-

mation from Brand, who estimated that a well-developed floating leaf of *Nymphœa lutea* was about eleven times the dry weight of a submerged leaf of the same area.

Another dicotyledon, *Proserpinaca palustris*, which was investigated by Burns, gave experimental results pointing to the same general conclusion as those already quoted. The primitive type of leaf in this plant is always a "water" leaf, but this type of leaf was also produced in the autumn by all the plants, regardless of any external conditions which the experimenter could control. On the other hand, at the time of flowering and in the summer generally, almost every plant, whether growing in water or air, produced the "land" type of leaf—the transition from the "water" to the "land" type taking place earlier on strongly growing than on weak stems. The author considers it evident that the aquatic environment is not the cause of the division of the leaf, nor does it depend on light, temperature, gaseous content of the water or contact stimulus. The only conclusion which he holds to be justified by his experiments is that *Proserpinaca palustris* has two forms, an adult form and a juvenile form; under good vegetative conditions, it tends to produce the adult form with the undivided leaf, the blossom and the fruit, while, if the vegetative conditions are unfavorably influenced, a reversion can be induced to the primitive form with the submerged type of leaf. These results are consistent with those of McCallum, who had dealt with the same species at an earlier date, but his interpretation is slightly different. He is inclined to regard the occurrence of the water form as induced by the checking of transpiration and the increased amount of water which hence accumulates in the protoplasm. This explanation is not inconsistent with the more general view that any condition tending to lower the vitality may be responsible for a reversion to the submerged type of leaf.

In nature, the regression to the juvenile type of leaf sometimes occurs, not only in the case of an entire plant subjected to adverse conditions, but also in the case of lateral shoots from an individual which is otherwise producing the mature form of leaf. Goebel for instance, examined an old example of *Eichhornia azurea* (Pontederiaceæ) which had wintered as a terrestrial plant in a greenhouse; the leaves were of the mature form, differentiated into sheathing base, petiole and lamina, except in the case of a lateral shoot, which, on the contrary, bore the grass like, simple leaves which characterize the young plant. Goebel also

describes the occurrence of subdivided leaves of the water type on lateral shoots of normal land plants of *Limnophila heterophylla*. A corresponding reversion has been observed in the case of the side branches of plants of *Proserpinaca palustris* developing *in the air* from a plant whose main stem was producing the mature type of leaf; by removing the growing apex of the stem in June, side branches of the "water type" were induced to develop.

The interest of these lateral shoots, which show a reversion to an *ontogenetically* earlier type of leaf, is enhanced by the fact that C. and F. Darwin in "The Power of Movement in Plants" have recorded a case of the occurrence, on lateral shoots, of leaves whose characters are probably *phylogenetically* earlier than those which the species normally exhibits. Their observations related to the sleep habits of the allied genera, *Melilotus* and *Trifolium*. They noticed in *Melilotus Taurica* that leaves arising from young shoots, produced on plants which had been cut down and kept in pots during the winter in a greenhouse, slept like those of *Trifolium,* with the central leaflet simply bent upwards, while the leaves on the fully grown branches of the same plant afterwards slept according to the normal *Melilotus* method, in which the terminal leaflet rotates at night so as to present one lateral edge to the zenith. They suggest that *Melilotus* may be descended from a form which slept like *Trifolium*.

The idea that the "juvenile" leaves produced on lateral shoots may in some cases represent an ancestral type, is consistent with the facts in the case, for instance, of the Alismaceæ, provided that the "phyllode theory" of the monocotyledonous leaf be accepted in the sense advocated by Professor Henslow and the present writer. According to this theory, the ancestral leaf of this family was ribbon-shaped, while the oval or sagittate blade (or "pseudo-lamina") represents a later development—a mere expansion of the apex of the petiole. The submerged youth leaves of this family would thus represent a reversion to phylogenetically older forms.

If the interpretation of heterophylly indicated in the present paper holds good at all widely, the teleological view of the submerged leaf must be considerably modified. The present writer would like to suggest that, for the old conception of heterophylly as *induced* by aquatic life, we should substitute the idea that such a difference between the juvenile and mature forms of leaf as would render the juvenile leaf well suited to aquatic life, has been

in many cases one of the necessary preliminaries to the migration from land to water, and that the aquatic angiosperms thus include, by a process of sifting,[1] those plants whose terrestrial ancestors were endowed with a strong tendency towards heterophylly.

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## COALESCENCE OF THE SHELL–PLATES IN CHITON*

CHITONS are peculiar in the fact that the molluscan shell is here represented by a series of eight distinct dorsal plates, which in different genera overlap and articulate with one another to varying degrees. The full number, 8, seems, however, to be invariably present. While examining recently a series of somewhat over 2,100 individuals of *Chiton tuberculatus* L., I came upon two cases, and two only, exhibiting any irregularity with respect to the number of the shell-plates. These were specimens, a male and a female, found near together on the beach at Cross Bay, Bermuda, in which plates 7 and 8 had in each instance almost completely fused (Figs. 2–6), so that each of these animals seemed at first sight to have but 7 plates; since no records seem previously to have been made of such occurrences, they are here figured and described.

In the two abnormal chitons the fused terminal plates were of similar external appearance, but in individual A, the female, the coalescence of plates 7 and 8 was somewhat less complete than in individual B, the male, as shown by the form of the inner surfaces of the compound plates. It is perhaps accidental that in both cases fusion of the respective plates is somewhat assymetrical, being more complete on the right side. As seen in Fig. 4, the muscular intersegmentum, which ordinarily receives the insertion plates of the eighth valve, is represented by a relatively small tongue of tissue.

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[1] We owe to Dr. H. B. Guppy, F.R.S., the important idea that the habitats of plants are determined by their peculiarities of structure and not *vice versa*. In relation to the occurrence of plants with buoyant seeds and fruits in water-side stations, he writes, "there are gathered at the margins of rivers and ponds, as well as at the sea-border, most of the British plants that could be assisted in the distribution of their seeds by the agency of water. This great sifting experiment has been the work of the ages, and we here get a glimpse at Nature in the act of selecting a station."

* Contributions from the Bermuda Biological Station for Research, No. 104.

It may be of significance that the only instances obtained of fusions of the kind figured, occurred at a sandy beach, on the south side of Bermuda, exposed to the beating of the ocean surf.   Individual A, when found, was attached to a rock, but was half-covered by sand left by the tide.   Chitons in such situations are frequently buried for a time beneath a foot or more of sand, and under these circumstances the over-lapping edges
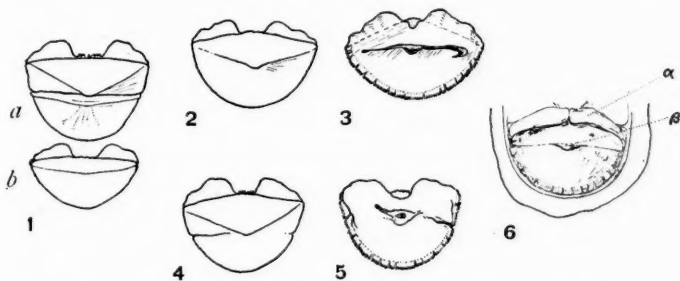


FIG. 1.   Outlines of valves 7 and 8 of a normal *Chiton tuberculatus;* a, in their natural relations; b, plate 8 separately.   Natural size.

FIG. 2.   Compound terminal plate of an abnormal *C. tuberculatus* (individual A, ♀) 4.4 cm. long; dorsal view.   Natural size.

FIG. 3.   The same, ventral view.   Natural size.

FIG. 4.   Compound terminal plate of an abnormal *C. tuberculatus* (individual B, ♂) 4.5 cm. long; dorsal view.   Natural size.

FIG. 5.   The same, ventral view.   Natural size.

FIG. 6.   Dorsal aspect of posterior end of *Chiton A*, to show (β) reduction of intersegmentum 7–8; (α) intersegmentum 6–7.   Both abnormal chitons estimated to be five years old.   Natural size.

of the shell-plates are kept tightly pressed together, thus preventing sand-grains from abrading the soft inter-tegmental mantle.   The posterior end of a *Chiton tuberculatus* is less active in turning movements, in curling-up and in similar operations than is the anterior end, so that two valves, once stuck together, might, at the posterior end, have a better chance of remaining together.   The incomplete union of the valves, visible when seen from their inner side, suggests that the coalesced plates started out independently.   Whether or not this view be valid, it would be of interest to determine if there is any general tendency, in special localities, toward the establishment of races of chiton possessing a reduced number of plates.

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## THE EFFECTS OF THE WINTER OF 1917–1918 ON THE OCCURRENCE OF SAGARTIA LUCIÆ VERRILL[1]

In June, 1902, I published in the American Naturalist some notes on the dispersal of *Sagartia luciæ* that tended to show that this sea-anemone had spread from the neighborhood of New Haven, Conn., along the New England coast as far north as Salem, Mass. This migration was accomplished in approximately a decade, from 1892 to 1901. Since 1902 repeated efforts have been made to discover evidences of this species farther to the north than Salem but without avail. Apparently the species had reached its northernmost limits.

*Sagartia luciæ* was first noticed in Woods Hole, Mass., in 1898. From that year until the present it has been an extremely abundant species on the stones, mussels and eel grass in the waters of this region. On Pine Island, a narrow ridge of rocky gravel overtopped with coarse vegetation and lying in the swift tidal currents of the Hole, the narrow beaches between tides have been covered with thousands of this species of sea-anemone. When this locality was visited in June, 1918, not a single specimen of *Sagartia luciæ* could be found, though the particular area examined had been covered with many individuals the year before. Nor was this condition due to the relatively early date at which the search was made. Repeated attempts during low tides in July and August never yielded at Pine Island more than two or three specimens at a time, and it was quite clear that *Sagartia luciæ*, once so prevalent in that locality, had suddenly become all but extinct there. The same was true of other situations in and about Woods Hole. In fact, a general search showed that in not a single location where this sea-anemone had been abundant in 1917 could there be found more than a paltry number of specimens in 1918.

The occasion of this sudden and great diminution in the numbers of *Sagartia luciæ* is to be attributed, I believe, to the rigor of the winter of 1917–1918. The cold and ice of this winter were almost unprecedented. Mr. Vinal Edwards, the veteran collector of the laboratory of the United States Bureau of Fisheries at Woods Hole, has kept a continuous record of the weather conditions of this region for a long period and this record shows, as might be expected, that the winter conditions in 1917–1918 were more severe than for many years past. In no win-

[1] Contributions from the Zoological Laboratory of the Museum of Comparative Zoology at Harvard College.

ter during the last ten years has the sea water been at 0° C. or lower for so long a period as last winter. Beginning with the season of 1908–1909 and proceeding to that of 1917–1918, the number of days for each of the ten winters in which the temperature of the seawater was 0° C., or lower, was 3, 40, 44, 63, 3, 55, 0, 65, 36 and 80. Thus 1917–1918 with its 80 days of extremely cold water strikingly outruns any one of the preceding nine years.

This winter was conspicuous for the formation of large amounts of anchor frost in the shallow waters about Woods Hole. This frost or ice can be seen forming on the bottom of shallow bodies of salt water when the temperature of that water is at 0° C., or lower. It is apparently due to the freezing of fresh water that, seeping through the land, rises from the sea bottom and solidifies at once on coming in contact with seawater below its own freezing point. This fresh-water ice is especially destructive to marine animals on the bottom and its great prevalence during the winter of 1917–1918 is probably responsible for the scarcity of sea-urchins and other like forms the following summer. It probably had little or no effect on *Sagartia*, for this sea-anemone lives chiefly between tides and, therefore, above the level at which anchor frost is found, but as a winter phenomenon this ice is a good index of severity and it is severity in the nature of low temperature that is responsible, I believe, for the almost complete elimination of *Sagartia*.

That this sea-anemone was not destroyed by the merely mechanical effect of ice and waves is seen from the fact that the same stretches on Pine Island that were populated with *Sagartia luciæ* were, and still are, covered with many specimens of *Metridium marginatum*. This northern species seems not to have suffered in the least from the severity of the past winter and I, therefore, conclude, since *Metridium* was as much exposed to mechanical injury as *Sagartia* and still survived m ordinary numbers, that *Sagartia* succumbed to low temperature rather than to any other factor in its environment. This is in accord with the general belief, originally expressed by Verrill, that *Sagartia luciæ* is a southern species introduced by some accident into northern waters. Granting this conclusion, it is easy to understand why this species has not migrated farther northward into colder waters and why in severe winters it is almost exterminated in localities such as Woods Hole.

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# TAXONOMY AND EVOLUTION

## A Rejoinder

THE writer has great sympathy with much of what "X" has to say on the above subject in a recent number of the AMERICAN NATURALIST (Vol. XLVIII, 369–382).[1]   Needless to say, however, he can not  agree with all.   True there is much in systematic zoology that is slipshod, but till statistics can be produced to show that the percentage of slipshod work produced by systematic zoologists is higher than in other fields of zoology, the writer of this article has a temporary residence in Missouri. He is of the opinion, also, that as great a percentage of the work of the systematic zoologist will stand the test of time as the work of the anatomist or any other worker in the field of zoology and proposes to remain of that opinion until time, the great leveler, proves to the contrary.

Linnæus is apparently not the only genius that has left the back door open and that has "been followed by a crowd of other workers eager to attain to immortality," as witness the great mass of half-digested literature on genetics, say, that has been crowded into the past ten or a dozen years.   It would be a sad state of affairs indeed if systematics as a whole were not improving.   That there have been occasional backward steps there is no doubt, but on the whole the progress has been forward. I hardly believe that even the systematists are as big fools as "X" pictures them to be, for I have yet to discover in my rambles a systematist who believed that his work was final. Heaven forbid.   The czar in zoological nomenclature may arise and issue his fiat, but there will be later czars who will do away with them.   For surely "X" would not have us believe that the day will ever dawn in this world when all things are settled. My shorter catechism is somewhat awry, but surely such a happy state is reserved for the Great Beyond.

Without wishing to disparage the modern workers I wish to say that some of the older workers did write "careful descriptions," as witness the following case which has been called to my

[1] The present paper was written in July, 1914, soon after reading the paper by "X." It was laid away but now that it is more than four years old "going on" five, as children say, it seems best to submit it for publication.

attention.   One of the early systematic entomologists described a species, on external characters only, in about three lines. Later entomologists were puzzled because the species had characters common to two widely separated genera; and one systematist said it belonged to one genus, and another said to a widely divergent genus, while a third said it was simply another name for a common form.   Yet, behold, when the species was redis-covered it was found to belong to a new genus with characters common to the two widely divergent genera.   Now, what's the answer, certainly the original description must have been a good one otherwise how could workers nearly a century later rec-ognize the characters?

Isolated quotations from descriptions of any species look ridiculous (p. 370), but no more so than isolated quotations from the work of ecologist, neurologist or what not.   A kindly feeling for my fellow workers in other fields and for the editor of the AMERICAN NATURALIST stays me from quoting at length and verbatim.   Fortunately "X" has sufficiently concealed his identity so that I can not quote some of his own discussions until he yawns.   Neither is my soul more deeply stirred by con-templating the poor hymenopterist, squinting at his box of dried "bugs" stuck on pins; than it is by the poor hunch-backed short-sighted cytologist (let us say) who, peering through his high power compound microscope, imagines that the world is circum-scribed by his field of view and that a cell, or a nucleus, or a chromosome, is all there is to zoology.

"X" seems to deplore the fact of specialization in zoology and at the same time seems to ignore the fact that it is along these lines that the world moves.   Why should we not have neurolo-gists, taxonomists, hemipterists, etc., in zoology just as we have masons, carpenters, roofers, painters, tinners, etc.   How many railroads would have been built in this world or how much progress would have been made in any other line of human en-deavor if every man had to be a jack-of-all-trades?   Do we hire a man to build us a house?   Most certainly not.   We hire a brick mason to lay the foundation, a carpenter to erect the frame, another one to put on the weather boarding, and still another to do the finishing inside; and so on until our house is finished and the whole structure stands only as long as the work of each one of these individual workers will stand.   So it seems to me it is in zoology, the systematist lays the foundation upon

which the whole structure is raised. And while the whole
method of systematic zoology is open to criticism by anatomists,
or what not, yet a certain amount of systematic work must be
done before the anatomist can develop his work. If we take
this position it seems to me that we must grant that the sys-
tematist must be far to the forefront, well in advance of the
workers in other fields. And certainly this much must be said
in his favor that he has turned out enough "new species" in
the last few years to keep the rest of the zoologists busy for a
year or two.

"X's" whole attitude is that the systematist makes mistakes
and that he sticks only to external characters. In regard to the
first I would call "X's" attention to the fact that anatomists a
little less than 300 years ago believed the arteries carried air, not
blood. And it seems to me if we go back about 250 years we find
one Robert Hooke describing "little boxes (empty) of cells dis-
tinct one from another"; and wasn't it only about half a century
ago that the cytologist awakened to the fact that the boxes were
not as empty as might seem? Now the question to my mind is
this, would we know as much about cytology as we know to-day,
if Hooke had not discovered his empty boxes? I think not.
And as a necessary corollary would we know as much about the
animal world as we now know if systematists had not described
new species? I think not. The fundamental basis of systematic
work, it seems to me, must always be external characters, though
they may be variable and unsatisfactory in many respects.
What we all want and what I believe all systematists are striving
for though some of their strivings may be misdirected is, among
other things, ease of identification which, to my mind, implies
reference to external characters. I see a woodpecker sitting in
a tree and identify him as a yellow-bellied sapsucker by the fact
that he has, among other characters, a white stripe down his
wings. Very unscientific, I grant, but highly satisfactory to me
if I am collecting not sapsuckers but downy woodpeckers. Also
to the sapsucker if the alternate character which enabled me to
identify him was the presence of extra small convolutions on his
cerebellum.

I make my plea for systematic zoology as systematic zoology,
not for its "phylogenetic classification of animals," nor for its
bearing on geographical distribution, variation or heredity or
anything else. The description of "560 new species of Zonitidæ"

may not seem soul-inspiring work to "X," but to the describer it may have been exceedingly so. The description of 560 new species of Zonitidæ makes it possible for some student of variation or of "phylogenetic classification" to work on the Zonitidæ in a way that would not have been possible if these 560 "new species" had not been described, and no one man would have been able to describe the 560 new species and work their embryology, internal anatomy, neurology, ecology, geographical distribulation, behavior, variation, mendelian relations, etc., and live to tell the tale.

Furthermore, if there is any man that has the aptitude to describe "560 new species of Zonitidæ" my benediction is "let him go to it." And while 585 of his "560 new species" may prove to be false alarms that have never been turned in, at the same time it does not seem to have occurred to "X" that he may be doing much less harm thusly employed than if he were rampant with scissors, scalpels and needles or with killing agents, stains and a microtome trying to discover the true inwardness of the Zonitidæ. I do not want to be misjudged by any one who may think that I am making a plea for slipshod work, but I do want to make a plea for the isolated worker who is plodding away in his own particular field without hope of reward or recompense in this day or generation. Let us be very careful about setting our stamp upon a thing as worth while or not worth while. Mendel, the poor isolated monk, working away with his peas, never dared dream, I venture to say, that his work would revolutionize the biological thought of the twentieth century. Thus "X" may have the misfortune to view in a future reincarnation the sad spectacle of the zoologists of say 200 years hence loudly acclaiming the good work of the describer of the 560 new species of Zonitidæ, while at the same time they point with scorn to the work of the anatomist who discovered (?) that the digestive system of the Zonitidæ runs up hill.

The writer has the fortune or misfortune, as pleases your point of view, to be the entomologist of a state experiment station. His principal duties as entomologist are the intensive studies of two widely separated species of extremely injurious insects. This work is carried on under the Adams Fund by grants from the United States Department of Agriculture. Both projects were so outlined as to involve everything about these

two insects that could be discovered by the writer; internal and external anatomy, embryology, life history, parasites, etc. Present indications are that it will take an average of about six years to finish (?) each one of these projects. Yet such a seemingly slow rate of progress is made possible only by the fact that some one working somewhere has described these two species and given them names. The one species was described without the describer ever having seen the male! Yet without this inadequate description progress on this problem would have been very greatly delayed. And so it is in every other field that these problems touch. Some one has described somewhere 29 species of parasitic hymenoptera, one of this number preying upon one of the species involved. Yet the describer knew only the adult and that only imperfectly, but his knowledge plus my own sends us one step nearer the complete knowledge of this species which ''X'' craves. And our knowledge of this species plus some one's knowledge of other related species raises us just one step nearer the truth which should be the goal of all human thought, and all science, zoology not even excepted.

I am interested in the phylogenetic relationship of a group of insects of no great economic importance. Especially am I interested in the genealogical tree of these insects as shown by the groups of characters of one structure. Now such work is made possible because three men in this country have devoted their entire time describing new species and new genera in this group. Without these descriptions many of which might have served as well as the one quoted on page 370, and without the collections of insects which these three men have made it would be impossible for me to make any progress along the line of a genealogical tree, which it is my fond hope will be of some use to the systematists of this group and to zoologists in general.

I have long wondered what could be called trivial characters. A few illustrations of the importance of so-called trivial characters in other fields than systematics may perhaps occur to ''X.'' One of the most important that has come to my notice was that of a cytologist who discovered differences in the chromosomal characters of two different sets of individuals of the ''same species'' only to discover later that systematists had long distinguished between these two forms on the basis of characters more trivial than whether they were ''pink with blue spots'' or

"blue with pink spots." Again two species of scale insects are separated by the fact that one has the median lobes of the pygidium rounded while the other has the median lobes conical (external characters). Yet one lives on oak trees and has at least four generations annually and the other lives on maple trees and has only a single generation annually. Now if "X" thinks that these facts would have been discovered as easily and as quickly as they have been discovered, if Professor Comstock had not pointed out these "trivial characters" some thirty-odd years ago, he thinks differently than I think. Yet the application of these facts is of vast importance to the horticulturalist and landscape architect or any other artisan who works to beautify our landscapes with trees, or any one who attempts to control these two pests.

I have no doubt that Linnæus was accused of relying on trivial characters for separating some of his genera and species. It would be interesting if history could tell us and it would be still more interesting if we could look into the future, say 100 years, and see what systematists and others will say about the present-day systematists who overlooked such perfectly obvious characters as the extra spines on the hind leg of species "a" as contrasted with "b" and their wonder and amazement that systematists of this our glorious twentieth century should have overlooked such important and obvious characters. So it will be in other fields. The histologist of the future will wonder why we used such crude killing and fixing agents; and will, more than likely, refer to our finest precision microtomes with a shrug much as we refer to the stone hatchets of the men of the Old Stone Age.

I make this somewhat extended plea because it seems to me that "X" has unconsciously done the systematists a great wrong.[2] "X's" attitude may discourage promising young men from entering the field of systematics where their help is greatly needed. Let us therefore lay aside our critical air and our sitting in judgment to decide just what is worth while and what isn't and turn our attention to utilizing the results of other workers in other fields to the greatest extent. The systematist

[2] That all may see that my plea is entirely unselfish, I will state that I am not a systematist and that I have never described a single "new species." My attitude is simply one of gratitude to the systematists who have helped me with my problems.

is human like the rest of us, he has his limitations like the rest of us, but he believes, I think justly, that his work is pioneer work of great importance; and, if occasionally he gets beyond the limited range of our embryologist's microscope or our anatomist's scalpels and needles, let us not accuse him of wandering along the River of Doubt or being a lineal descendant of the famous Baron Munchausen. But let us look upon the systematist's work as the foundation for the glorious structure, modern zoology, which completed by his other co-workers will stand four square to the wind for all time to come. We do not need to defend systematics on the basis of "(1) the advertisement theory; (2) the recognition mark theory;" although both are perhaps more important than "X" intimates. But what is vastly more important is the fact that systematics is the basis for all real work in zoology. And the morphologist or anatomist who takes the attitude that systematics is to be entirely avoided[3] or, what is worse, is to be simply laughed at is placing himself in the same class as the man who says that there is no such thing as matter in the world. Sooner or later he is going to bump into the fact that systematics must play its part in his field and that systematics is broader than the question whether the "second joint is longer than the third" or whether a species should be called aabus Smith or beabus Jones.

Z.

[3] Just what does "X" think about the anatomist who discussed at great length the anatomy of, let us say, the "American frog (*Rana temporaria*)" because that was the name given the frog in his perfectly good English "Text-book of Zoology"; when the context shows that the frog he was dealing with was the common leopard frog (*Rana pipiens*)?